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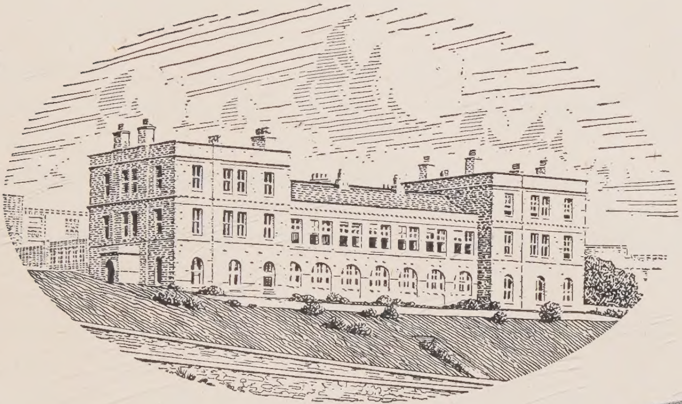

THE PLYMOUTH LABORATORY

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BOOK NOTICE

The German Hydrographic Journal 277

ERRATA

Page 70. Line 13, *for* Clarke *read* Clark.

80. 9 lines from bottom, *for* east *read* south-west [of Beachy Head].

81. Table III, figures for mean 1937–9, *for* 7542, 21,798, 6895, *read* 6680, 14,843, 4701.

335. Last line, *for* Stevens *read* Steven.

449. Line 20, for *guttorugine* read *gattorugine*.

580. 8 lines from bottom, *insert* bottom *between* marine *and* invertebrates.

719. Table II. For [*Mullus*] *surmulletus* read *surmuletus*.

THE DISTRIBUTION OF *GAMMARUS* SPECIES IN ESTUARIES. PART I

By G. M. Spooner, M.A.
Zoologist at the Plymouth Laboratory

(Text-figs. 1–7)

Editor's note. This paper and that by Dr S. G. Segerstråle (this *Journal* pp. 219–44), independently bringing forward certain new ideas on the taxonomy of *Gammarus zaddachi* and *G. locusta*, were received for publication simultaneously. As this paper is a report of work largely carried out before the war, of which summarized results have already been referred to in print (e.g. Report of Council in this *Journal*, Vol. XXIV, pp. 444, 691; Huxley, *The Modern Synthesis*, p. 315), it is given precedence. The authors have since consulted each other over matters in which their contributions overlap, in particular over the taxonomic status of the new forms they distinguish and regarding the names to be applied to them. Dr Segerstråle has kindly consented to adopt the two new names introduced by Mr Spooner. In this paper, where appropriate, footnotes giving cross-references to Segerstråle's paper have been inserted.

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INTRODUCTION

The work of which an account is here given was largely carried out from the autumn of 1937 to the spring of 1940, when it was interrupted by the war. In taking it up again (in July 1945) while facilities for field work are still limited, the author feels it useful to publish results as they stand and indicate where further work is considered advisable.

In examinations of the free-swimming bottom fauna of the Tamar and other estuaries, attention was inevitably drawn to the populations of *Gammarus* species, which make up the greater bulk of it. Before quantitative observations were planned, some interesting points came to light with regard to the qualitative composition of populations. This aspect lent itself more readily to study and, though by no means a new field for exploration, soon proved worth examining in greater detail than previous workers had attempted.

The broad fact of a replacement of one *Gammarus* species by another in passing up an estuary was well enough known, though exact knowledge for the British Isles only starts from the time when *G. zaddachi* Sexton was recognized as a regular member of the upper estuarine fauna of the Tay (Bassindale, 1933; Alexander, Southgate & Bassindale, 1935) and of the Deben (Serventy, 1935). This species proved to be the main brackish-water species overlapping with the marine *G. locusta* (L.) near the seaward end, and with the fresh-water *G. pulex* (L.) at the river end (or 'head') of the estuary. The status in estuaries of two other brackish-water species, *G. duebeni* Lillj. and *G. chevreuxi* Sexton, remained obscure. It has usually been suspected that salinity conditions are the critical feature of the environment which limits the range of a species in a given area; but Serventy suggested that exclusion through competition limits *G. zaddachi* to the middle reaches of estuaries, while there are known instances, and growing evidence of others, of one species having varying salinity tolerance in different parts of its geographical range. Such problems clearly demanded further study.

Much depends on accurate knowledge of the systematics of the genus. Thanks to the work of Sexton in this country, workers are now in a strong position to identify British material. Yet, as will become clear in the pages which follow, there were (and are) still facts to be added, and confusions to be rectified.

There are several advantages in the choice of *Gammarus* as a subject for ecological study, some of which have only become fully appreciated during the course of the present work. (1) They are among the more abundant of estuarine animals. (2) Being adaptable to varied surroundings and not limited to specialized ecological niches, they do not show gross patchiness of distribution within their habitable range: for example, a continuous population occupying the whole length of an estuary or lagoon can usually be found, even though the proportions of species represented change from one end to the other. (3) Furthermore, it can be said that they are indifferent to the nature of the substratum to a remarkable degree. Provided there is some kind of object which can provide them with cover or shelter, it matters not whether the bottom is muddy or stony, the water turbid or clear. Almost any kind of organic matter provides detritus on which they can feed. This means that, in so far as inanimate environmental factors limit distribution, affect growth rate, or produce any difference between two populations, these are mainly to be sought amongst the more elementary properties of the environment, such as temperature, salinity, and oxygen concentration. (4) The brackish-water species, at least, can be reared in the laboratory and subjected to controlled experimental conditions.

METHODS

The use of a box sieve makes collecting a simple matter, and overcomes the difficulty of samples getting fouled with mud. The sieve actually used is similar to that designed for handling mud samples, as described by Spooner & Moore (1940). It forms a cube of 1 ft. each way, the bottom made of perforated zinc, the sides of wood, and the top open. A window of perforated zinc in one of the sides facilitates outflow of water. Suitable handles are fitted on each side at the top.

In estuaries, clumps of weed or any other suitable objects, collected from the ground in the intertidal zone or from the bed of the river channel, are placed in the sieve and well shaken in water, the sieve held three-quarters submersed. The larger objects and fragments are shaken out and discarded in turn. The macrofauna which had been contained in them accumulates at the bottom of the sieve with a mass of small fragments and debris. This is well washed by lifting the sieve in and out of the water, and transferred as desired to collecting jars. It is easy to perform these operations without injuring the animals, though care must be taken when gravel or small stones accumulate in the debris. When working in ditches or pools it is often useful to make the collections of weeds, etc., in a strong fine-meshed net, but the net contents should always be sieved, as this is the only effective method of removing mud and of concentrating the catch.

A final washing of the samples may be necessary on return to the laboratory, so that when they are placed in bowls (in appropriate mixtures of sea and fresh water) the contents are free from turbidity. Normally gammarids will comprise the greater bulk of the catch. Animals are killed by addition of strong formalin solution, and preserved in 5% neutral formalin in sea water. Samples were always examined as soon after killing as possible, while the normal colours remained unimpaired.

Examining live, or freshly killed, specimens enormously facilitates rapid diagnosis. Sometimes colour characters, lost after preservation, are valuable taxonomically—the most spectacular example, perhaps, being the orange pigment spots in *G. locusta* immature (see p. 14). In other respects, also, characters seem more easily assessed in fresh specimens, while the tissues still retain their transparency. It is clear that if amphipodists generally were able to concentrate more on fresh material, some of the existing taxonomic difficulties and confusions might never have arisen.

As a preservative, formalin is far superior to alcohol, in which specimens often become very opaque, hard and brittle. The formalin should, however, not be dissolved in water of much lower osmotic concentration than that of the body fluids; otherwise, swelling of soft tissues is apt to occur. A solution of 5 % formalin in sea water is perfectly suitable for marine and brackish-water organisms, and, as far as I have tested it, for fresh-water Crustacea as well. Specimens so preserved can always without harm be placed temporarily in tap water for examination.

Microscope mounts of limbs, etc., are conveniently made in a chloral medium, e.g. Faure's Solution, as used by entomologists. No preparation is necessary; the chitin is cleared of soft matter in a short time; the medium hardens sufficiently to make ringing the mount optional; and the preparations normally keep indefinitely. Also if at any time remounting is considered desirable, the mount is simply dissolved in water. Slides intended for more temporary use can be mounted as rapidly as in water, with the advantage that they do not dry up and can be kept permanently if subsequently desired.

Apart from collections made personally, various material collected by other zoologists has been examined, and I am particularly indebted to Mrs E. W. Sexton, Mr G. I. Crawford, the late Dr K. Stephensen (Copenhagen), Prof. A. D. Hobson, Dr L. C. Beadle, Mr R. Bassindale, Mr R. Elmhirst, and Mr H. P. Moon, for the loan or presentation of material. It is a pleasure to record my thanks to Mrs Sexton for her constant interest and for the ready loan of her specimens and literature. Mr G. I. Crawford has sent me material from the British Museum, including samples collected by himself after leaving Plymouth; his earlier collections (see Crawford, 1936, 1937) were available for examination at the Plymouth Laboratory. Mr R. Bassindale's interesting series of samples from the Severn Estuary has already been recorded and commented on in the 'Studies on the Biology of the Bristol Channel' publications (Bassindale, 1941, 1942*a*, 1942*b*, 1943). Prof. Hobson's material included collections from the Inner Hebrides, from streams flowing on to the shore, of which an account is published by Beadle & Cragg (1940).

I wish further to thank Dr Sven Segerstråle for his most helpful co-operation before our respective papers were finally printed.

TAXONOMIC OBSERVATIONS

It was not possible to proceed far with ecological observations without first going rather thoroughly into the taxonomic aspects of the species under consideration. The chief reasons for this were as follows.

(1) Species of *Gammarus* tend to differ in a number of minor characters in addition to any major differences which may exist. These were repeatedly examined, not only to obtain knowledge of their constancy or variability, but for the more immediate purpose of detecting atypical populations. Sometimes differences, though small, prove remarkably constant and reliable, and are invaluable when specimens are atypical, for some reason or other, in important respects (for example, as a result of stunted growth, inhibited maturity, or regenerating limbs), or with parts missing as a result of damage. It is needless to emphasize that the larger the number of characters available, the stronger is the position of the investigator.

(2) It was very desirable to determine reliably, not merely adult males, for which alone, as a rule, detailed descriptions are available, but individuals of both sexes at all ages. This aspect had to be given special attention, and some original observations are reported below. It was gratifying to find that reasonable characters exist to separate the immature of all species which are liable to occur together in Britain, even down to the smallest growth stages of which account has been taken. The necessity for dealing with specimens of all sizes also demanded closer recognition of the changes which take place during the course of life, particularly during the late immature and early maturity stages. Characters of animals whose development is gradual and whose growth continues throughout life are profitably studied in their four-dimensional aspect.

(3) Even with adult males of British species it was soon apparent that some existing descriptions were still not complete, and that the true value of some diagnostic characters had still to be adequately assessed. It was also possible to separate *G. zaddachi* into two readily identifiable subspecies, which, in addition to their morphological differences, have very different salinity optima.

(4) Most character-differences are comparative. It was intended at least to make a start in expressing some of them more precisely in numerical and statistical terms.

Note on the numbering of the peraeopods

It is necessary to emphasize that one change in descriptive terms has been adopted. Sexton (e.g. 1912, 1942) and Sexton & Spooner (1940) still follow Sars (1895) and Stebbing (1906) in numbering the peraeopods from peraeon segment 3 onwards, so that the limb of segment 3 is peraeopod 1 and of segment 7 is peraeopod 5. Hoping that this confusing habit will soon be abandoned altogether, I propose to follow the more logical and (by now) more general practice of giving the limbs the same number as the segment (as in Chevreux & Fage, 1925). Thus the gnathopods, which are the limbs of peraeon segments 1 and 2, are the modified peraeopods 1 and 2; the first unmodified limb, or 'leg', is peraeopod 3; and the hindmost limb, that of peraeon segment 7, is peraeopod 7. The term 'peraeopod' simply means the limb of a peraeon segment and has no functional implication, whereas the terms 'gnathopod' and 'leg' are functional and denote special forms of peraeopod. It is unfortunate that authorities like Sars and Stebbing have used the terms 'leg' and 'peraeopod' in exactly the reverse sense.

Species in estuarine and associated faunas

The following species have occurred in faunas examined in this work:

Marinogammarus marinus (Leach, 1815).
M. obtusatus (Dahl, 1938).
M. finmarchicus (Dahl, 1938).
M. stoerensis (Reid, 1938).
Gammarus locusta (L. 1758) G. O. Sars, 1895, *sens.str.*
G. zaddachi Sexton, 1912, typical subspecies, as here designated.
G. zaddachi salinus, subsp.nov.
G. chevreuxi Sexton, 1913.
G. duebeni Lilljeborg, 1851.
G. (*Rivulogammarus*) *pulex* (L. 1758).

Marinogammarus species

The taxonomy of these essentially marine littoral forms has already been dealt with (Sexton & Spooner, 1940). At the same time a list of the material examined up to the summer of 1940 was included. Stephensen (1940) also gives descriptions and locality records, especially from Norway. Certain additional British material has since been examined; for example, collections made in 1942 and 1943 on the shore near the Millport Laboratory, where five of the species occurred (see Scottish Marine Biological Association, *Annual Report*, 1942–3, pp. 10–11).

In estuaries *M. marinus* alone has been encountered in abundance, extending well into the mid-estuarine reaches. It is, however, much concentrated near high-water levels, and does not enter into the low-water and mid-channel populations to which main attention is subsequently given. More will be said later, from an ecological aspect, about the upward limit of penetration into estuaries, a point which is fairly easily determined by inspection in the field.

M. olivii (M.-Edw.), of which a description was included in our 1940 paper, had not at that time been recorded from Britain. Almost simultaneously, however, Reid (1940) reported it from the River Avon in South Hants, where, at Keyhaven, it was living in water which was fresh to slightly brackish (see also Goodhart, 1941). This species, however, is not a widely spread inhabitant of estuaries and is probably extremely local.

Gammarus locusta (L.) G. O. Sars, *sens.str.*

This abundant marine species has been well enough recognized from descriptions in standard works (e.g. Sars, 1895; Della Valle, 1893; Stebbing, 1906; Chevreux & Fage, 1925) so long as purely marine faunas were under examination. In the seas of western Europe there seems to be no species with which it is liable to be confused. But in estuarine and brackish faunas it has been much confused with *G. zaddachi salinus* (pp. 20–1). Existing descriptions are still in need of amplifying to emphasize certain characters which have proved important in distinguishing typical *locusta* from other known species, and to indicate more clearly what variation occurs amongst genuine *locusta* populations.

It is necessary to emphasize that this account applies only to the *locusta* of the temperate eastern Atlantic and the North Sea (and apparently also to the western Mediterranean). I have recently been able to satisfy myself that the form occurring in northern waters (west Norway, Iceland, Greenland, Newfoundland and Arctic coasts) differs in so many respects that it is quite separable.[1] It is possible also that the form of the species which inhabits the western Baltic in much lower salinities than are tolerated, for example, in Britain, may genuinely be less easily separated from *G. zaddachi* in that area.[2] A fuller treatment of the characters of *G. locusta* in its whole range is deferred for a later occasion. The description here, however, is valid for the form which seems to be generally accepted as the type of *locusta*, following the drawings by Sars (though his description by itself is not critical enough).

Adult male

In addition to the descriptions in standard works, Sexton (1942, pp. 600–1, pl. iii, figs. 19–24) gives a list of characters useful for comparison with related species, as well as new drawings of the head, antennae and gnathopods. Only certain comments need be made. In *antenna* 1 the long accessory flagellum is a valuable diagnostic character, especially if consideration is given to the allometric changes which occur during growth. At the onset of maturity it has 7 or 8 segments which increase to 13 or 14 in the largest and oldest individuals. At the start it is about 1½ times the length of peduncle segment 2, but it soon attains twice the length of that segment, and in the end is about 2⅓ times as long. As compared with *G. zaddachi salinus*, young males have about 2 segments more, the oldest about 5. In antenna 1 peduncle the length ratio of 3:2:1 for the first three segments is always closely approached.[3] In

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[1] In essential respects these northern animals seemed much closer to *zaddachi*. Segerstråle (pp. 223 *et seq.*) has independently shown that they are to be included under that species. The description of *zaddachi* has only to be modified in minor respects to include this form, whereas that of *locusta* would need to be drastically revised.

[2] But see comment on p. 18.

[3] Precise micrometer measurements give ratios of 142–153:100:45–49 for the three segments, segment 3 being consistently rather less than half segment 2.

other species segment 1 is always less than the combined length of the other two, and the 3rd is often longer than half the 2nd. *Gnathopod hands.* Once the fully mature adult stage has been reached, the form and arrangement of the palmar spines of both gnathopods are diagnostic and easily recognized. This character should, as always, be given primary weight in critical determinations. The gnathopods are well figured for the first time by Sexton (1942, pl. iii). (N.B. Sars's drawing, 1895, pl. 176, fig. 1 p²♂, is inaccurate, and was probably taken from a specimen of the northern form.) *Gnathopod 2 hand.* The exact shape of this segment is somewhat variable, though it is normally in some sense longer or narrower than in *zaddachi* and *duebeni*. While both the dorsal border and the palm are relatively long, the ventral border is less so; thus the palm tends to approach the length of the ventral border, especially in larger and older animals. The ventral border may diverge somewhat in an apical direction, or at least remain straight and parallel with the dorsal border: only infrequently is it rounded towards the palmar angle in a manner typically found in *zaddachi*. More significant is the arrangement of the palmar spines (Fig. 1). The median palmar spine is succeeded, towards the palmar angle, by a regular series of spines graded in respect to size and distance between successive spines. This arrangement contrasts with a condition more frequently met in *Gammarus* species (including *G. zaddachi*,

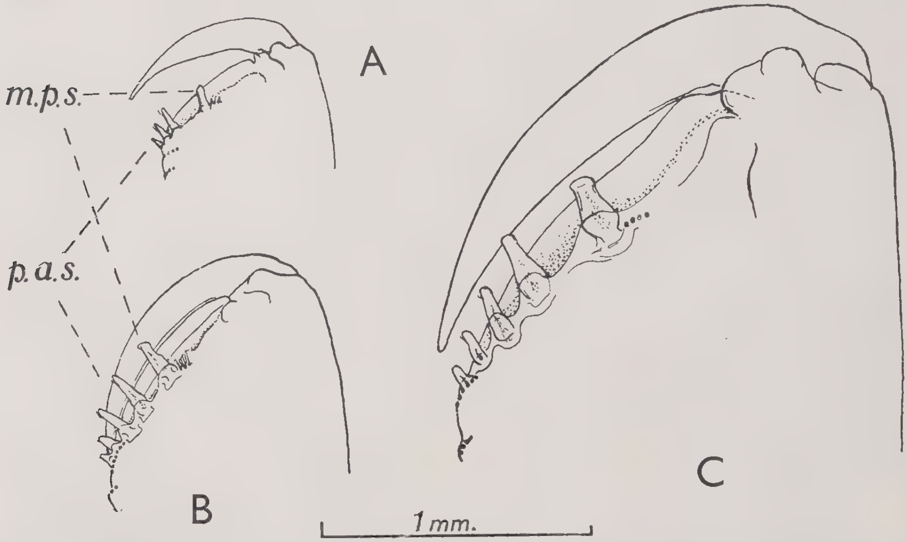

Fig. 1. *Gammarus locusta sens.str.*, male gnathopod 2 hand, distal part, with hairs omitted, to show the arrangement of the palmar spines. A, young mature male, Saltash, River Tamar, 5. iv. 38, showing the median palmar spine (*m.p.s.*) still separated from the palmar angle spines (*p.a.s.*). B, larger and fully mature male from same sample. C, large male, 25 mm., Plymouth Sound, 12. xi. 06. In B and C all the spines tend to form a continuous row with graded intervals.

and the earliest mature stages of *locusta* itself, Fig. 1 A), where an isolated median spine is separated by a marked gap from a cluster of spines arising quite close together at the palmar angle. Only *G. duebeni* (p. 37) shows a graded series at all comparable. It is important to appreciate that the true *locusta* pattern is not finally attained until two or three growth stages after maturity have been reached. Another important characteristic of mature *locusta* hands is seen in the truncate tip and bulbous base of the median palmar spines, and of the larger of the angle spines, which thus become almost 'flask-shaped' (those of *duebeni* retain their original simple shape). *Peraeopods* 6 *and* 7 (examples of *Pp.* 7 in Fig. 2): in these limbs the more apical segments are often provided with some long, stiff, outstanding setae, arising singly or in sparse tufts, particularly noticeable on the middle part of the pre-apical segment (propodite). The posterior border of the basal segment, however, is at most sparsely furnished with short setules. The hair pattern can thus be distinguished from both subspecies of *G. zaddachi* (p. 23 and Fig. 4). All limbs tend to be somewhat elongate and slender compared with other species of the genus, with the exception of *G. wilkitskii* Birula, in which they are more extremely so, and of *G. zaddachi* which differs very little. Peraeopod 7 shows this tendency at least as much as other limbs, and has been selected for standard measurements. The length (*a*) of the carpopodite has been compared with (*b*) its width at the first proximal spine group, and with (*c*) the length of the basal segment. The ratio of $a:b$ is 4·0 to 4·5; of $a:c$ is 0·75 to 0·80. The last ratio is lower in other species considered here; the first lower in all but *zaddachi*. The *telson*, in conformity with the limbs, is also relatively elongate. In adult males the length of one arm is 2·4–2·5 times its greatest width (in immatures and very young males it is still of more normal proportions with the ratio at about 2·0). *Uropod* 3 *inner ramus* is typically subequal in length to the outer ramus: more precisely, it is typically 96–99% the length of the first segment of the outer ramus. No other marine or brackish water *Gammarus* in British waters shows this condition, and only occasional large specimens of *G. zaddachi salinus* even approach it (p. 29). But some populations, especially those subjected to reduced salinity, have an appreciably shorter inner ramus, which may remain as low as 85% in well-developed adults. This variation, whether genetic or environmental, is best thought of as an arrest of the differential growth of the inner ramus; since the latter starts much shorter than the outer ramus and normally steadily catches up on it, or nearly so, during the immature phases. The *urosome segments* dorsally are characteristically strongly raised and laterally compressed in the median line. The elevations are angulate, those on the first two segments forming a right angle in contour, or nearly so (90–110°). In no other form are these elevations so pronounced.

In practice the relatively long accessory flagellum, the proportions of antenna 1 peduncle segments, the form of the hand of gnathopod 2, the dorsal elevations of the urosome, and the long uropod 3 inner ramus, together or

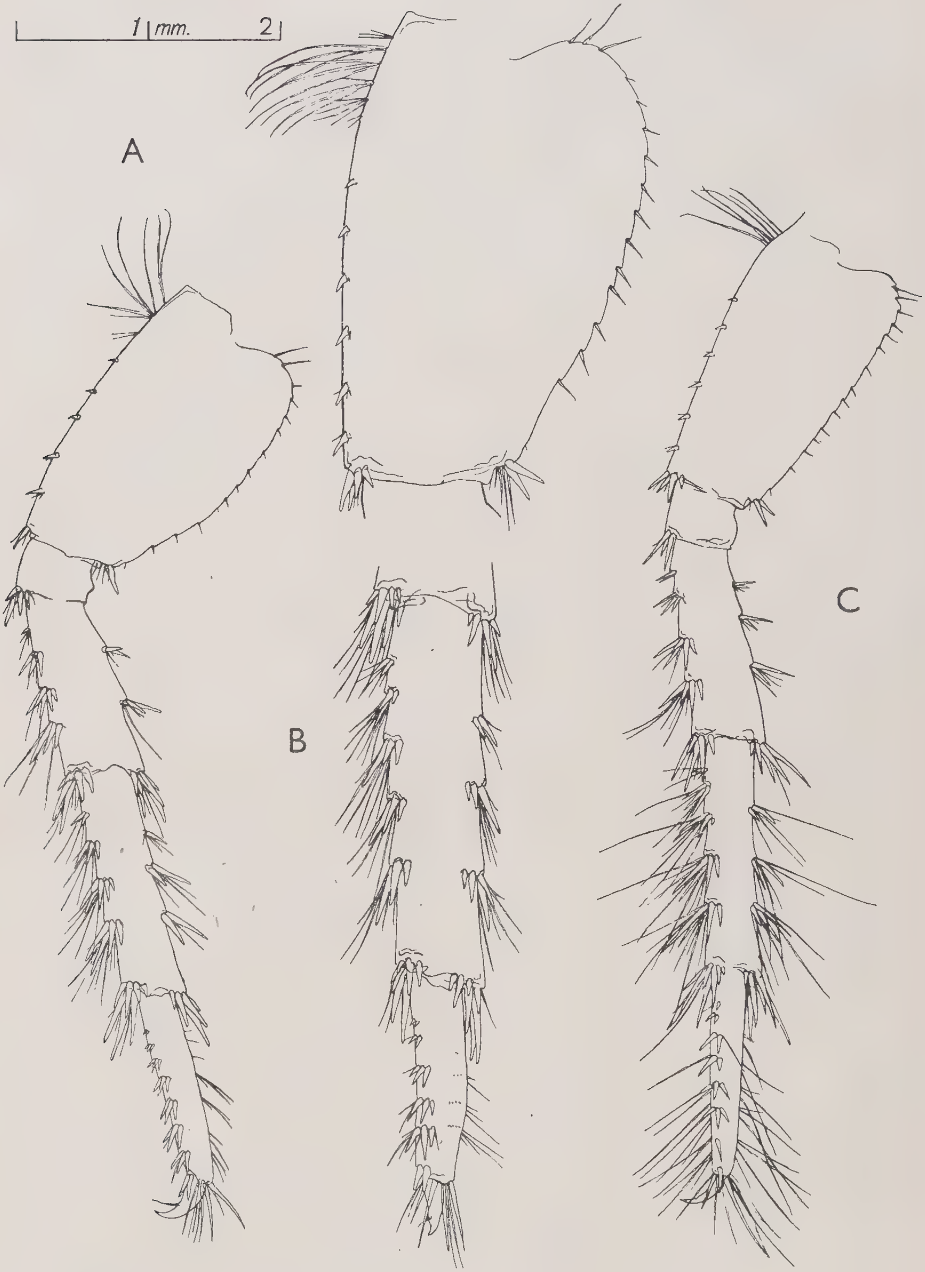

Fig. 2. *Gammarus locusta sens.str.*, peraeopod 7 of male (coxopodite omitted). A, Saltash, River Tamar, 5. iv. 38 (larger specimen than in Fig. 1). B, Plymouth Sound, 12. xi. 06 (same specimen as in Fig. 1), middle segments omitted. C, variety from the Fleet, Dorset, near Langton Herring, 14. xi. 37.

even individually provide quick means of identification. The sparseness of the hairs on antenna 1 peduncle ventrally provides a critical distinction from *G. zaddachi.* Good specific characters also show in the shorter head, the sharply angulate ventral corner of its lateral lobe, the elongate anterior coxal plates, the deep and subrectangular ventral portion of coxal plate 4, and the much produced and pointed inferior angles of epimera 2 and 3. In fresh material the presence of orange pigment spots on the mesosome segments (see below) is also diagnostic, though in larger adults these may be reduced, or absent, or obscured by dense epidermal pigmentation.

Adult female

Most of the characters given for the adult male apply equally to the female. The description has only to be modified in respect to (1) characters which are directly concerned in sexual dimorphism, e.g. the presence of brood-plates, and the structure of the gnathopod hands; and (2) characters which involve appreciable allometric changes during early maturity, and which remain closer to the immature condition in the more conservative female.

The *size* attained is much less than in the male: in south-west England a maximum of 20 mm. length (head to apex of telson) contrasts with 28 mm. maximum in the male. The *accessory flagellum* of antenna 1 in the very largest individuals has 11 segments, when it is 2·2–2·3 times the length of peduncle segment 2. More usually the larger specimens in samples are of the order of 15 mm. body length, and these have an accessory of 8 or 9 segments and of length about twice, or slightly less, that of peduncle segment 2. On *antenna* 2 the flagellum lacks calceoli. The *gnathopod hands*, though much less specialized than in the male, have still some taxonomic value: the hand of gnathopod 2 is unusually elongate, its dorsal and ventral borders very straight and parallel to each other, and its length always more than twice its distal width (in no other form is a ratio of 2·0 exceeded; in *G. zaddachi* it is 1·65 to 1·8). The median palmar spine is lacking. On *peraeopod* 3 the hairs are sparser than in the male. The limbs are less slender than in the male adult: in peraeopod 7 the carpopodite is 3·5–3·9 times as long as broad proximally, and only 0·66–0·70 the length of the basal segment. The *telson* length attains only 2·25 the greatest width of one arm (though this is still longer than in related species except *G. wilkitzkii*). The *urosome* elevations are not quite so pronounced as in the male. The *body pigmentation*, though variable, is usually heavier, a deep blackish blue colour, with pale bands on the antennae, being common. The *eggs* are relatively small (see below), and the numbers in one batch relatively large: as many as 235 have been taken from a specimen of 20 mm. length, and 230 from one of 16 mm.

In mixed samples the female *locusta* is at once distinguished from *zaddachi* by its sparse antennal hairs, its more elevated urosome segments and its elongate gnathopod 2 hand.

TABLE I. DIMENSIONS OF EGGS IN *GAMMARUS LOCUSTA* AND *ZADDACHI*

Gammarus locusta

Sample	Length of female mm.	Size of brood	n = no. of eggs measured	Mean length (l) × width (w) mm. × 10^{-1}	Calculated volume cu.mm. × 10^{-2}
			Newly laid and early development stages		
b	8	23	22	4·429 × 3·691	3·16
b	8	14	13	4·848 × 3·632	3·35
b	8·5	22	22	4·669 × 3·822	3·57
b	8·5	25	23	4·810 × 3·791	3·62
b	10	44	40	4·678 × 3·792	3·52
m	16	230	40	4·502 × 3·668	3·17
e	13·5	57	40	4·632 × 3·786	3·48
e	15	163	25	4·614 × 3·981	3·83
d	—	68	40	4·630 × 3.938	3·76
d	12	84	83	4·735 × 3·916	3·80
b	10	29	23	4·842 × 3·958	3·97
b	10	12	9	4·96 × 3·91	3·97
f	10	24	23	4·797 × 3·617	3·29
m	13·5	135	50	4·746 × 4·018	4·01
b	9·5	28	28	4·857 × 3·986	4·04
b	10	29	27	4·836 × 4·003	4·06
			Intermediate development stages		
e	13·5	106	40	5·138 × 3·946	4·19
e	16	219	80	4·728 × 4·123	4·21
l	—	38	30	4·995 × 4·160	4·53
			Embryos advanced		
d	13	80	25	5·302 × 4·416	5·41
e	—	46	45	5·307 × 4·484	5·59
b	12·5	31	15	5·355 × 4·437	5·52
b	9	8	8	5·420 × 4·500	5·75
b	9·5	12			
			Young well-formed or ready to hatch		
b	9	*c.* 27	8	5·70 × 4·55	6·18
b	9	14	6	5·68 × 4·83	6·93
d	—	78	25	5·661 × 4·618	6·32
d	12	65	25	6·045 × 4·781	7·23
f	10	32	25	5·907 × 4·656	6·71

Index to samples from which females were taken:

a, River Tamar, Thorn Point, 22. vi. 39.
b, River Tamar, Thorn Point, 9. x. 45.
c, River Tamar, Ernesettle, 1. iii. 38.
d, River Tamar, Henn Point, 5. iv. 38.
e, River Tamar, St John's Lake, 5. v. 38.
f, River Plym, Laira Bridge, 23. xi. 46.
g, River Erme, near mouth, 8. ii. 39.
h, River Avon (South Devon), 16. v. 38.
i, River Avon (South Devon), 8, i. 39.
j, River Avon (South Devon), 20. v. 46.
k, Kingsbridge Estuary, Blank's Mill Creek, 22. i. 39.
l, Kingsbridge Estuary, Salcombe, viii. 45.
m, Brancaster, Norfolk.

TABLE I (*continued*)

Gammarus zaddachi *

Sample	Length of female mm.	Size of brood	n=no. of eggs measured	Mean length (l) × width (w) mm. × 10^{-1}	Calculated volume cu.mm. × 10^{-2}
Newly laid and early development stages					
a	—	12	8	5·42 × 4·44	5·59
a	—	19	17	5·393 × 4·659	6·13
c	11	44	44	5·573 × 4·720	6·50
c	10·5	20	20	5·720 × 5·080	7·73
c	12	22	21	5·989 × 5·067	8·05
c	11	22	20	5·856 × 5·120	8·04
i	10	32	32	5·680 × 4·725	6·64
h	13	62	25	5·594 × 5·005	7·34
k	9	20	19	5·726 × 4·855	7·07
k	9·5	22	22	5·855 × 4·800	7·06
k	9·5	31	29	5·639 × 4·935	7·19
Intermediate development stages					
a	—	7	3	5·84 × 4·96	(7·52)
h	7	14	11	6·044 × 4·909	7·63
i	10	33	32	5·898 × 5·065	7·92
i	*c.* 10	29	19	5·924 × 5·040	7·88
i	—	32	28	5·880 × 5·286	8·60
g	—	14	10	6·347 × 5·184	8·93
Embryos advanced or young well formed					
i	—	37	7	6·24 × 5·51	9·92
h	7	14	8	6·52 × 5·30	9·59
h	10·5	45	35	6·421 × 5·518	10·23
i	11·5	42	34	6·506 × 5·544	10·47
h	13·5	—	5	6·88 × 5·52	(10·98)
h	9·5	25	20	6·872 × 5·740	11·86
Young about to hatch					
c	11·5	31	13	7·92 × 5·60	*c.* 13·0
	14	40	10	7·120 × 5·944	13·17

* All specimens belong to subspecies *salinus* (see p. 20).

Measurements of eggs

A number of measurements of batches of eggs from females of *locusta* and *zaddachi salinus* are given in Table I to show the contrast between the two forms. Individual measurements were made in units of 0·008 mm. From the greatest (l) and narrowest (w) diameters, a value representing the volume has been calculated from the formula $l \times w^2 \times \frac{1}{6}\pi$. It will be observed that the volume is about 0·55–0·6 that of *G. zaddachi* eggs at comparable stages of development. If there is any increase in size of egg with size of parent, this must be very small and negligible compared with other sources of variation. On the other hand, as is well known, the average number of eggs in one batch tends to increase with the size of the parent. The young at extrusion are correspondingly smaller than in *G. zaddachi*.

Immature

Almost from the time of hatching a small cluster of reddish orange pigment globules is present on several of the peraeon segments. These are situated on segments 2–7 in the body wall near the base of each limb (Fig. 3). Similar, usually more elongate and more diffuse, patches occur on the metasome, but these are common to several species of *Gammarus* and *Marinogammarus*. The presence of these coloured spots on the peraeon is diagnostic of *Gammarus locusta*. As the young and immature are otherwise colourless and translucent, the spots are very obvious in living and freshly preserved specimens. Though after maturity these pigment spots may be reduced or obscured, they are almost constantly present during immaturity, and provide an excellent means of identifying fresh material, particularly in sorting, for example, mixed populations of *locusta* and *zaddachi*. This is an example of a character which might be thought to be of low taxonomic grade, but which has proved very reliable in practice.

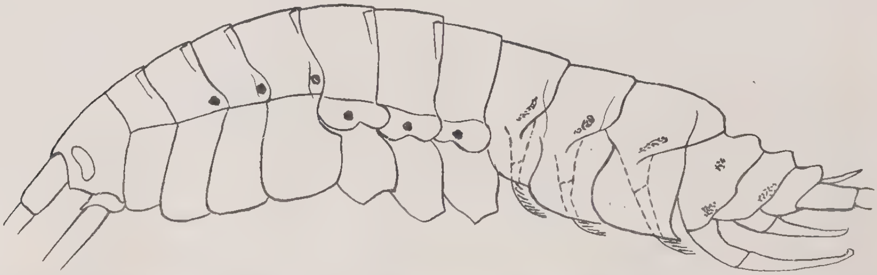

Fig. 3. *Gammarus locusta sens.str.*, body in side view, semi-diagrammatic, to show the position of the orange pigment patches in the body wall. The patches on peraeon segments 2 to 7, which are diagnostic of this species, are shown as rounded black spots.

By the time the immature phase is about half-way through, *locusta* can be distinguished from other species by various structural features. Already there are indications of a relatively long accessory flagellum, raised urosome elevations, and produced epimera. The inner ramus of uropod 3 is long enough to distinguish it readily from that of a *Marinogammarus*. *Gammarus duebeni* is already isolated by the conspicuous produced posterior angles of peraeopod 7 basal segment. The main structural difference from *zaddachi* at this stage is in the hairs on the ventral surface of the antennal peduncles, which in *zaddachi* are by now longer and more numerous.

While male characters are developing in the maturing animal, until the stage at which the fully mature form is reached (two or three stages after functional maturity), the hand of gnathopod 2 is still of a somewhat generalized type (Fig. 1A). The median palmar spine has appeared, but, as in other species at this stage (and in most throughout life), it is still separated by a gap from the spines at the palmar angle, and is not fully truncated distally. Other heterogonic changes are going on at this time, and in very young males comparative measurements may not yield ratios found to be characteristic of the full adult. For example, values nearer those of the female are found for the relative lengths of carpopodite 7 and the telson. In the female the relative length of the gnathopod 2 hand increases from 2·0 to about 2·3 during the first stage of maturity.

Notes on variation within the species

Apart from adult body pigmentation and average size, the character which perhaps varies most noticeably in normal populations concerns the development of hairs on the limbs. This variation, however, is usually only evident after close inspection, and its range is limited. It seems to apply most to those limbs and side-plates where the total number of hairs is at best never large. For example, a sample from the north Norfolk coast near Brancaster is uniformly hairier, on all peraeopods and on the pleon, than Devon populations. But often within a single population quite noticeable differences occur between individuals of comparable stages of development. Though this matter deserves closer study, the general fact is clear enough, and shows that *locusta* is no exception to the rule that the development (i.e. number in a cluster, and length of individual hairs) is always subject to variation in a *Gammarus* species, perhaps sometimes as a more or less direct effect of environmental factors or nutrition, though such an effect has still to be demonstrated experimentally.

Among marine populations an interesting variation has been observed in a sample collected by Mr G. I. Crawford in Whitsand Bay, November 1934, by dredging in shallow water offshore. In one sample (5. xi. 34) the males have very dense setation on antenna 2 and peraeopod 3, and the longer hairs are much curved. Except that the elevations of the urosome segments are somewhat rounded and less compressed than usual, other characters are typical of the species. In a second sample of over 300 (dredged in weed, 16. xi. 34), which contained adults of all sizes, actively breeding, the same features are shown, but the male hairs are not quite so dense and only some of the hairs are curved.

It is, however, among populations living under recognizable atypical conditions that variations are most frequently observed. Some examples from brackish waters can be given.

At the limit of penetration into estuaries, particularly if conditions are deteriorating, as with the onset of winter, animals seem subject to inhibition of growth. Maturing individuals are smaller than usual, and often have a somewhat shortened uropod 3 inner ramus (retention of an immature character). It appears, however, that they soon die off as the salinity drops, and do not survive long enough to produce a persistent modified population. In the continuously habitable parts of estuaries populations resemble those from the sea. Those living in turbid water or on muddy bottoms are usually deficient in epidermal pigment, and tend to retain the immature translucent appearance.

In some localities where the species is established in water of permanently reduced salinity, persistent atypical characters may be shown. Two instances have come to notice: in the Fleet, Dorset, and New England Creek, Essex.

The Fleet is a shallow stretch of water separating the Chesil Beach from the mainland (see Tansley, 1939, chapter XLII, pls. 155, 156), receiving sea water by tidal action through its narrow connexion with Portland Harbour and fresh water by land drainage. Apparently a fairly steady salinity gradient is maintained through its 9-mile length, the incessant fluctuations characteristic of estuaries being largely lacking. At Langton Herring the water is salt enough to support *G. locusta* (in November it measured 26 °/₀₀ at low water). Samples collected here on 14. xi. 37 and 27. iii. 38 show the following characters. (i) Uropod 3 inner ramus short, in adult males only 80–90% of outer ramus segment 1; (ii) hairs unusually dense, especially in the male on antenna 2 peduncle and on hinder peraeopods (Fig. 2 C), the length and number of the stiff outstanding hairs on the latter being particularly noteworthy; (iii) the spines on ventral border of epimera 2 and 3 unusually strong; (iv) side-plates and basal segments of peraeopods (Fig. 2 C) notably narrow; (v) other segments of peraeopods slender, e.g. carpopodite 7 nearly 5 times as long as wide proximally; (vi) average size of adults below normal. All other features are quite characteristic of *locusta*; the male gnathopod 2 is in fact rather an extreme *locusta* type. The orange spots on the peraeon were well developed.

The population from New England Creek, Essex, where the fauna and environment were carefully studied by Howes (1939), is still more aberrant. Mr Howes kindly sent me his *Gammarus* for examination, and my report on their characters is given in his paper (p. 414). It is definitely a dwarfed population of *locusta*, presumably surviving from the time the creek was cut off from the sea by a dam. Ample diagnostic features are shown in the elevated urosome segments, the form of the male gnathopods, the deep ventral portion of coxal plate 4, the produced angular corner of the lateral lobe, the lack of long hairs on basal segments of peraeopods 6 and 7 (though the rest of these limbs is unusually hairy), the sparsity of hairs on antenna 1, etc. Atypical features recorded were as follows: (i) uropod 3 inner ramus relatively short, between 80 and 90% of segment 1 of outer ramus; (ii) hairs unusually dense, even more so than in the Fleet population; (iii) the spines on the ventral border of epimera 2 and 3 in some specimens notably strong; (iv) size much reduced, correlated with which the number of segments in the accessory flagellum did not exceed 8, 7 being a frequent number; (v) in one sample containing the most extreme dwarfed and hairy specimens there was a strong tendency for the hairs on the male antenna 2 to become curled.

It will not escape notice that the variations of these two brackish populations are of a very similar kind. One is tempted to ask whether reduction of salinity alone has not brought about like results in two widely separated localities. It would be very instructive to test the constancy of the characters of populations as these, by rearing in the laboratory under controlled conditions.

Two samples from the shore at Traigh Mor, Barra, Outer Hebrides (coll. K. M. G. Fleming), varied from the normal in the following respects: eye notably broad; hinder peraeopods with long spinose setae; female gnathopods and fore-peraeopods more densely hairy; and body size somewhat reduced.

Material examined

(Samples involved in population analyses to be dealt with later are marked with an asterisk. Abbreviations: coll., collected by; Coll., collection.)

England and Wales. E. CORNWALL: Whitsand Bay, 5. xi. 34, 16. xi. 34, samples dredged in shallow water by G. I. Crawford. E. CORNWALL and S. DEVON: Plymouth Sound, including Cawsand Bay, various samples on different occasions, including a large sample of well-grown adults from a dense 'swarm' in the open water of the Sound, 12. xi. 06 (Plymouth Laboratory Coll.); Estuary of R. Tamar and branches, numerous samples,* from the Hamoaze and St John's Lake upstream to Weirquay and Bere Ferrers. S. DEVON: various samples* from the seaward end of the estuaries of R. Plym, R. Yealm, including the Cofflete branch, R. Erme and R. Avon; from the shore at Wembury; from the Kingsbridge Estuary; and from the estuaries of R. Exe and R. Axe. DORSET: The Fleet, at Langton Herring, 14. xi. 37, 27. iii. 38, numerous amongst *Zostera hornemanniana* in water of reduced salinity; Lulworth Cove, 26. xiii. 37. S. and N. SOMERSET: Bristol Channel coast at Kilve and Weston (Severn Estuary survey, by R. Bassindale, etc., see references given on p. 39). S. ESSEX: New England Creek, dwarfed population in brackish water (Howes, 1939). N. NORFOLK: sample from Brancaster district, coll. C. F. A. Pantin. NORTHUMBERLAND: Blyth, ditch from salt pans, 4. vii. 34, coll. Prof. A. D. Hobson, adults, breeding (with *G. zaddachi salinus*). DURHAM and N.E. YORKS: River Tees Estuary, Tees Survey material* (Alexander *et al.*, 1935), several from tidal zone and in tow-nettings. ISLE OF MAN: Port Erin, shore and 4–5 fathoms, Port St Mary, in weeds near L.W., ix. 38, coll. G. I. Crawford.

Scotland. PERTHSHIRE and FIFESHIRE: R. Tay Estuary, Tees Survey material,* one male from tidal zone of Section XI. CLYDE ISLES: Cumbrae, Kames Bay, R. Elmhirst Coll., 6. iv. 34, a few adults. ARGYLLSHIRE: Clachan Strand, under weed, Prof. A. D. Hobson Coll. INNER HEBRIDES: S. Rona, vii, viii. 37, Prof. A. D. Hobson Coll., 'Dry Harbour', 10 fathoms, 4 ♂♂, 1 imm., 'Big Harbour', shore, small ♂ and ♀, 1 imm.; Raasay, viii. 37, A. D. H. Coll., Churchton Bay, 2–3 fathoms, a number, 'Stephenson's Bay', 1 ♂ (with *G. zaddachi*); Isle of Muck, A. D. H. Coll., in eight samples, from Gallanach, 1. ix. 36, 17. viii. 39, Port Chreadhair, vii. 38, Rudha Caem na Caraich, 30. vii. 38, 16. viii. 39, etc. OUTER HEBRIDES: Barra, coll. K. M. G. Fleming, vii. 36, 37, Traigh Mhor, L.W.S.T., two samples with adults of small average size.

Belgium. Ostende, Bassin de Chasse, *c.* 900 ♂♂, 870 ♀♀ and 400 imm., in 71 samples (in collections identified for the Brussels Museum in Jan. 1939).

Gammarus zaddachi Sexton

This is an important species in the economy of estuarine and other brackish waters, being very widespread in spite of the discontinuity of its habitats, and usually plentiful provided there is adequate cover of some sort and, apparently, an adequate oxygen concentration. It is one of the dominant members of the fauna in those parts of estuaries where the salinity fluctuations are greatest, and so most 'rigorous' to life.

The confusion over this species in the past has been considerable. Even after it had been described (Sexton, 1912), British material was still being overlooked and recorded as *duebeni* in fresher habitats, or as *locusta* in more saline waters. Continental authors have not helped matters, either from attempts to sink the species, or, sometimes, in their failure to appreciate its most reliable diagnostic characters.

Sexton (1942) has followed up her careful original description with a further detailed account which emphasizes (1) the differences between *zaddachi* and related species with which it may possibly be confused, and (2) the differences between the two extremes of variation, i.e. between a very hairy 'fresh-water' form inhabiting the lower reaches of the Elbe and Weser, and a sparsely haired, more spiny, 'true brackish water' form living in estuaries and along the coast of East Prussia. The 'fresh-water' form is figured for the first time. The presence of intermediate forms linking the two extremes is stressed. A complete and very valuable summary of the past literature referring to the species is also given. Those who wish to study *G. zaddachi* from any aspect are fortunate in having Sexton's admirable descriptive papers as a background.

There should no longer be any reason for confusions which have invalidated species identifications in the past, at least as concerns Britain. I have to concede that systematists may have a more difficult task in some other parts of Europe. For example, it is now clear that *G.* '*locusta*' in west Norway mainly belongs to a northern race which, though larger, is very close to *G. zaddachi* in its body proportions and gnathopod characters (see below); while, judging from published data on *Gammarus* populations from the west Baltic, I can only conclude that populations of *G. locusta* which occur there in low salinities fail to show some of the marked characteristics found in the typical form inhabiting the North Sea, etc.†

The need for giving yet further attention to the taxonomic characters of *G. zaddachi* arises from several causes. (1) Sexton's descriptions and drawings are based primarily on German material: the extent to which they strictly apply to British populations had to be examined. (2) The descriptions are mainly devoted to adult male characters: more complete knowledge of the female and immature had to be acquired, and a clearer picture obtained of heterogonic changes which take place during early maturity. (3) Most important of all, the variation which occurs within the species, at least some aspects of it, demanded attention; and one result has been to show that the species can be split into two well-defined types, as was apparent at an early stage in this investigation.

In erecting two subspecies, I am anxious to be able to refer to type specimens and type localities. Since no type of the species has ever been designated, it is necessary to rectify this omission first. Sexton's original description (1912) covers the species as a whole: selection must therefore be made from the samples she examined and described. For various reasons I choose the samples of the Hamburg 'fresh-water' population to designate the type of the species (Sexton, 1912, p. 660, 'Hamburger Wasserleitung', 5 specimens; Hamburger Wasserleitung, Samuelson, 71 specimens; Hamburg Mus. Coll.). These automatically become the types of the relatively 'hairy' subspecies, namely, *G. z. zaddachi*, which is now recognized as embracing a widespread form which colonizes brackish waters of low salinity, as well as fresh waters to a much more limited extent. Sexton's 'pure brackish water form' becomes subspecies *salinus*, with the type from the estuary of the River Weser: 'Bremerhaven, Herr Klie; Alterhafen, x. 1911' (Sexton, 1912, p. 660, pls. lxxiii, lxxiv). *G. z. salinus* is a characteristic estuarine form in west Europe, intolerant both of full-strength sea water and of water which is fresh or very weakly brackish. It is possible that further investigation will show that the so-called '*locusta*' from northern waters,[1] though essentially a marine form, should be included within *zaddachi* as a third subspecies.[2]

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† Segerstråle (pp. 219–44) has now made it quite clear why there has been so much confusion between *locusta* and *zaddachi* in Scandinavia and in the Baltic. His newly-defined (*z. oceanicus*) is in some ways intermediate between *zaddachi salinus* and *locusta sens.str.*

[1] Excluding *G. setosus* Dement., which is clearly a separate species. See also the footnote on p. 7.

[2] This is precisely the conclusion to which Segerstråle comes (pp. 223 *et seq.*). The northern marine subspecies occurs also in the Baltic as well as *salinus*, and I find that some of Sexton's original 'brackish water' form belong to it, as do also some British specimens from Scotland which I had formerly included under *salinus*.

THE DIFFERENCES BETWEEN THE TWO SUBSPECIES

	G. z. zaddachi	**G. z. salinus**
	Figures in Sexton, 1942: fig. 1*a*, pl. i (figs. 1–7), pl. ii (figs. 10–14)	Figures in Sexton, 1912, 1913, and 1942: fig. 1*b*, pl. i (figs. 8–9), pl. ii (figs. 15–18)
	Absolute differences	
Peraeopods 6 and 7 (setation)	With denser and longer setae: those on the posterior margin of the basal segment of peraeopod 7 are more numerous and much longer (a difference can even be seen in the larger immature). The long projecting hair tufts on the more distal segments are very conspicuous, especially in the adult male (Fig. 4 A, B; see also Sexton, 1942, pl. ii, figs. 10–12 for extreme form)	Much more glabrous, the more distal segments with only a few moderately long hairs at most, and the basal segment posterior margin with short setules. Conspicuous tufts on distal segments lacking. Spine groups more evident owing to sparsity of hairs and to greater average length of spines (Fig. 4 C; see also Sexton, 1942, pl. ii, figs. 15–17)
Urosome and telson (setation)	Similarly with longer and more numerous hairs (Sexton, 1942, pl. ii, fig. 13)	With a few shorter hairs only, which are rarely longer than the spines with which they are associated (Sexton, 1942, pl. ii, fig. 18)
Epimera 2 and 3	Posterior distal angles a little less acutely produced (Fig. 6 A). Epimeron 2 posterior margin with a row of several short setules (in adult male at least)	Angles rather more acutely produced (Fig. 6 B). Posterior margins of both epimera with not more than one or two setules

N.B. The characters given below regarding the length of the accessory flagellum and of uropod 3 inner ramus may provide absolute distinctions if animals from the same region are compared.

	Average differences	
General body colour of adult	Body pigment, when normally developed, distinctly dull greenish (with darker bands marking the boundaries of the segments); never infuscated	Body pigment, when developed, less greenish and more brownish (with obscurer banding); sometimes much infuscation may be found in the females (as in *G. locusta*)
Antenna 1 accessory flagellum	On average with one segment less (4–7 segments, according to age, in adults); somewhat shorter than peduncle segment 2, or at most about equal to it in older adults (see pp. 26–7)	On average with one segment more (5–9 segments, according to age); at maturity about same length as peduncle segment 2, becoming distinctly longer in older adults (see pp. 26–7)
Uropod 3 inner ramus	Relatively shorter; in majority (90 %) of British animals it is 0·67–0·76 length of segment 1 of outer ramus (see pp. 28–30)	Relatively longer; mainly (95 %) 0·78–0·89 length of segment 1 of outer ramus (Fig. 6 D)

THE DIFFERENCES BETWEEN THE TWO SUBSPECIES (*continued*)

	G. z. zaddachi	**G. z. salinus**
Urosome dorsal spines	Lower average number (see pp. 30–2). Average pattern in samples from south-west England: 2·2 2·0 2·2 2·5 2·0 2·5 2·05 2·0 2·05 (total: 19·5)	Higher average number. Average pattern in samples from south-west England: 3·15 2·4 3·15 3·25 2·1 3·25 2·5 2·0 2·5 (total: 24·3)
Telson spines	On average fewer; the subapical spine nearly always missing, and most frequently only two apical spines	On average more; the subapical spine typically present, and apical group nearly always with three
Peraeopod distal segments	In mature adults on average a little broader relative to their length, e.g. carpopodite of peraeopod 7 (in male) usually 3·1–4·0 as long as wide near its proximal end	In mature adults somewhat more slender, as in *G. locusta*. Carpopodite of peraeopod 7 ratio (in male) typically, 4·1–4·4
Gnathopod 2 hand of male	Normally a little more rounded and broader	Normally a little more elongate and parallel-sided
General setation	Hairs on antennae (Fig. 5), peraeopods 1, 2, 4, etc., on average longer and denser (more tufts and more hairs per tuft)	On average sparser and shorter (but rather variable particularly as between different localities)
Habitat	Inhabits the upper end of estuaries (roughly about the top third of the estuarine zone) and brackish waters of low salinities. In some areas can maintain itself under pure fresh-water conditions. Thus its salinity tolerance is lower	Salinity tolerance higher. Inhabits the middle reaches of estuaries where the salinity fluctuation is greatest, mingling with *G. locusta* at the seaward end, and with *G. z. zaddachi* towards the river end. Cannot tolerate fresh water

General setation

The typical subspecies tends generally to be more 'hairy' than *salinus*, both with regard to number of tufts, number of hairs in each tuft, and to the length of individual hairs. (On any given limb or somatic plate one of these features may be more relevant than the others.) It is now a matter of experience that 'hairiness' within a species of *Gammarus* is subject to local variation (e.g. the examples given for *G. locusta*, pp. 15–17, and similar behaviour in *G. duebeni* could be quoted), some of which may well be phenotypic, though this has still to be demonstrated experimentally. Indeed, there are some interesting variations within both subspecies of *zaddachi*, as here delimitated, more especially as between different areas or habitats. It is therefore necessary, on *a priori* grounds, to be especially cautious in attributing too great a taxonomic significance to differences in setation. On the other hand, the degree to which variation occurs in well-defined species appears to be subject to distinct limitations, and the general pattern and other features of the setation may provide useful diagnostic characters. This statement is necessary in view of Sexton's suggestion (e.g. 1942, p. 576) that characters affecting epidermal outgrowths should be treated in a different category from 'structural' characters (in which is included the shape of different parts and their relative proportions). From a purely morphological standpoint there seems no necessity for this opinion; while from a taxonomic approach it is enough to treat characters on their merits. By this is meant that when setation characters are found to present constant differences, these are of equal value with so-called 'structural' characters which show differences of comparable degree; while, conversely, both 'structural' and setation characters may equally be subject to a degree of variation which renders them unreliable taxonomically.

The variation in general 'hairiness' in *G. zaddachi* is known to be great, decidedly greater than in related species. But the range of habitats is also unusual, especially with regard to salinity. Sexton (1912, 1942) has emphasized the close correlation between the development of hairs and the salinity of the habitat, the hairiest examples having been found in fresh water, and the most glabrous in estuaries or brackish lagoons. Her interesting observations serve at least as a warning that variation in hairiness may be mainly phenotypic.

However, new light has been thrown on this subject by detailed study of *zaddachi* populations from Britain, where the difference between the more extreme hairy and hair-deficient individuals is comparable with that found on the continent. For the first time field study has been supplemented by experimental data. Present conclusions can be summarized as follows. (1) The variation in hairiness is not strictly continuous, but centres round two main types—representing the two subspecies as here defined. (2) The setation of the hinder parts of the animal shows a strong discontinuity between the two types, and provides a safe absolute means of separating them. (3) Estuarine populations of each subspecies, considered separately, fail to show any grading of hairiness correlated with the salinity gradient. (4) Since, also, the two types each retain their essential setation characters when reared at different salinities, the variation must be far from wholly phenotypic. (5) Since the two types are incapable of cross-breeding with each other, there is genetic difference between them; and on this genetic difference part of the variation in hairiness, observed in the species as a whole, must depend.

The use of certain setation characters has thus proved justified. At the same time it is necessary to be more precise than to consider hairiness of the animal as a whole. Variation in the setation of the hinder peraeopods, especially of the 5th, of the urosome, and of the telson, shows the greatest discontinuity, and is of special taxonomic value. This will be described in the next section. By contrast, the setation of the antennae (see Fig. 5), gnathopods, peraeopods 3 and 4, etc., while on the average showing fewer and shorter hairs in *salinus*, is too variable in different populations of each subspecies to be of comparable taxonomic value; though of potential importance in distinguishing some geographical or habitat forms. It is possible, for example, that the pure fresh-water populations may always be recognizable by a maximum development of hairs at the base of antenna 1 flagellum.

Setation of peraeopod 7, urosome and telson

Sketches of peraeopod 7 for adult males of both subspecies are given in Fig. 4. The essential features which separate the two forms are as follows:

G. z. zaddachi. (1) Basal segment with a row of hairs posteriorly, often of varying lengths, but with at least half of them distinctly long, often several times longer than the intervals between successive hairs. The number increases with the growth of the limb, but at comparable sizes this is somewhat greater than that of the short setules in *salinus.* (2) The hair-tufts on the mero-, carpo- and propodites are very conspicuous in the length and density of the hairs: the longer hairs in each tuft are at least twice the length of the longest spines of the associated group, and each tuft (excluding a few of the smallest) has at least 5 hairs, usually 8 or more. The posterior tufts on the propodite are at least half the length of the propodite itself.

G. z. salinus. (1) The posterior margin of the basal segment is provided only with short setules. These may be very short, or about as long as the interval between successive setules, usually distinctly shorter than the intervals. Normally they are more sparsely distributed than the hairs in the typical subspecies. (2) On the more distal segments the spines are more evident, partly because they tend to be somewhat longer, but chiefly because they are not overshadowed by the hair tufts. The latter are much sparser, reduced to 1 or 2 hairs (at most 3 or 4), of which only a single hair here and there may appreciably exceed the length of the associated spines. The posterior tufts on the propodite are similarly reduced, usually to 1 or 2 short hairs, but when less reduced the longest hair does not exceed one-third of the length of the propodite itself.

The spines in *salinus* have been noted as longer, as a rule, but it is doubtful whether the average number per group is greater.

Within each subspecies there is a limited amount of variation, as already indicated. For example, in *G. z. zaddachi*, both the length of the hairs and the density of the tufts appear to be at a maximum in the Hamburg fresh-water population described by Sexton (1912; 1942, pl. ii, fig. 12), but these can be matched by the 'hairiest' specimens found in British brackish waters. In Britain the populations from the Tay and Tees estuaries are on the whole distinctly 'hairier' than those from South Devon estuaries. The hairs of the latter, however, cannot be still further reduced by rearing in water of increased salinity. It seems that in them the limit of variation towards reduction of hairs in *G. z. zaddachi* has been reached.

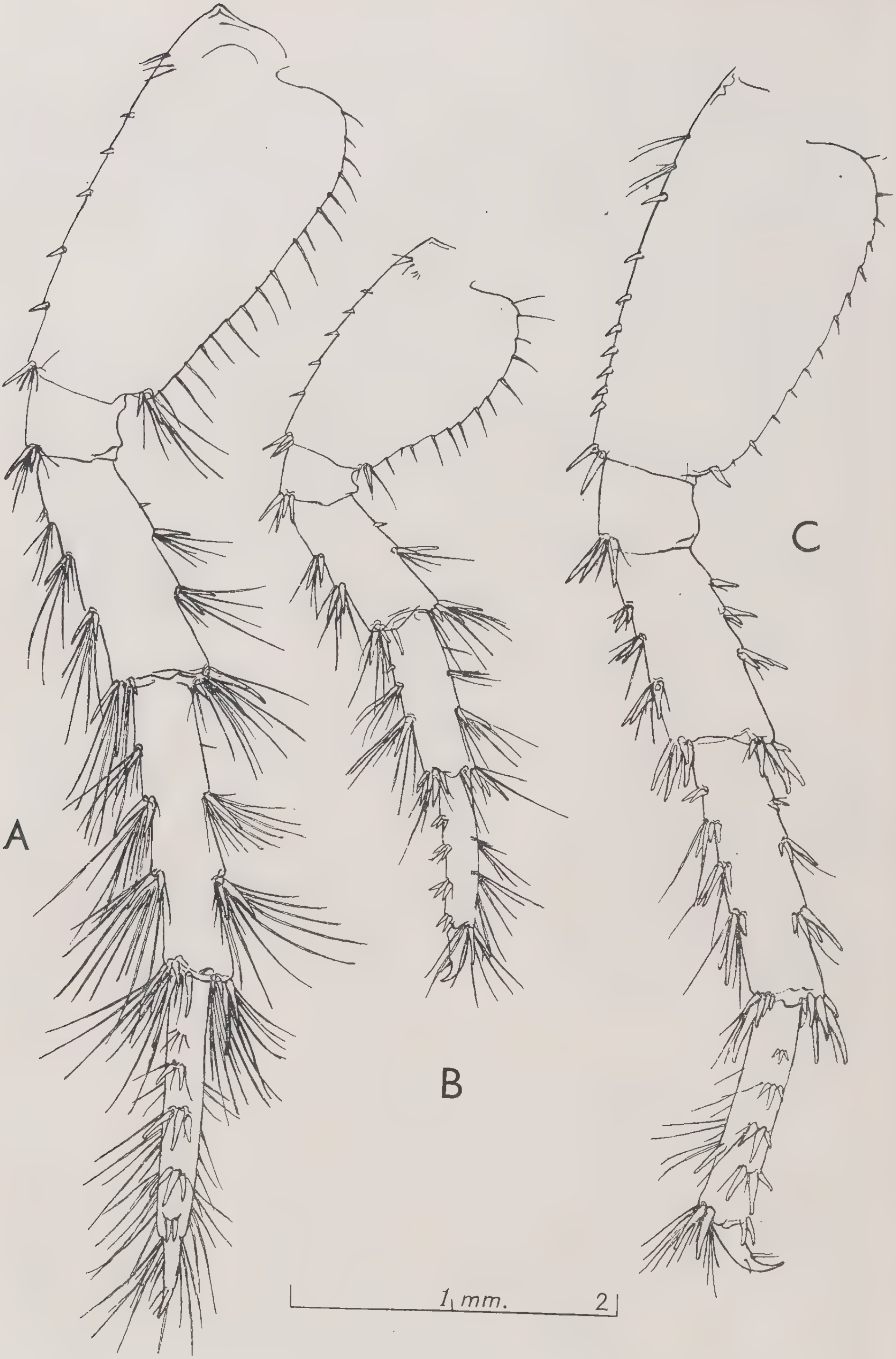

Fig. 4. *Gammarus zaddachi*, peraeopod 7 (coxopodite omitted). A, subspecies *zaddachi*, male (no. 52), Cofflete creek, River Yealm, South Devon, 3. vi. 46 (from moult). B, female of same, from the same sample (from moult). C, subspecies *salinus*, male, 18 mm., River Avon, South Devon, 14. v. 46.

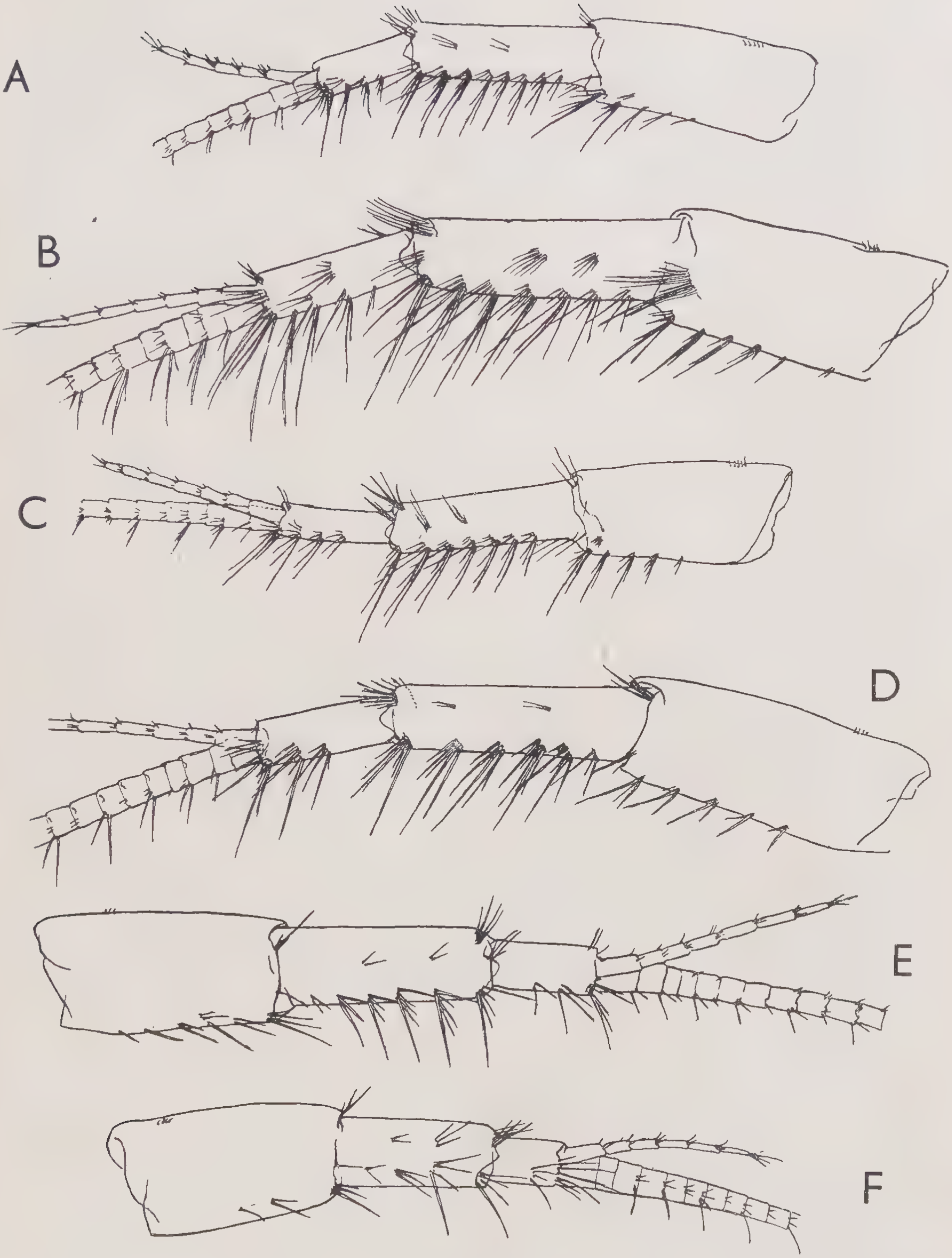

Fig. 5. *Gammarus zaddachi*, peduncle of male antenna 1; A–C, subspecies *zaddachi*, D–E, subspecies *salinus*. A, St John's, River Tamar, 28. iii. 40, 18 mm. B, River Tees, 21 mm. C, Cofflete creek, River Yealm, South Devon (from moult). D, River Severn, 23. vi. 39, 21 mm. E, River Avon, South Devon, 14. v. 46, 18 mm. F, River Tay, section IX. All viewed from inside, except B, in which the bases of the ventral tufts are shown as though seen through the thickness of the segments. (Note, in F, that segments 2 and 3 are relatively short compared with segment 1, and the ventral hair tufts, of which there are only two on segment 1, are relatively sparse.†)

† This compares with the northern subspecies described by Segerstråle on p. 226.

Altogether the variation within each type is not great, and would require rather detailed statistical study to demonstrate adequately. On the other hand, there is a clear distinction between any adult individual of *G. z. zaddachi* and any of *G. z. salinus*. For practical purposes the sketches illustrate the contrast as well as any description can attempt.

In females the difference is comparable, but not so striking, as that described for adult males, since the density of the hairs in *G. z. zaddachi* (Fig. 4 B) is not so great. But even in the youngest females and in the more advanced immature stages a difference is perceptible. During later immaturity the appearance of the first few hairs (which are short at this stage) on the posterior margin of the basal segment is the first character to distinguish the typical subspecies from *salinus*.

Peraeopod 6 shows very similar characteristics to peraeopod 7, but has been less closely studied. There seems, however, to be rather more variation in its setation, and it is certainly not so useful in separating the two subspecies among younger animals.

As regards the urosome and telson, there is a comparable absolute distinction between the two subspecies, at least when the two parts are considered together. In *G. z. zaddachi* the urosome dorsal spine groups each produce a tuft of long hairs which are at least half as long again as the spines themselves. In each group there are at least two hairs for every spine present, often more. In the telson the hairs are similarly long and numerous; the subapical spine is nearly always absent and replaced by 2–5 long hairs; the apical hairs protrude well beyond the spines and are usually numerous enough to be difficult to count. In *G. z. salinus* the hairs are shorter and quite sparse: on the urosome there are not more than one for each spine present, often less, and these do not exceed the spines in length. On the telson only one or two of the apical hairs are apt to protrude a little beyond the spines. Elsewhere it is shown that *salinus* tends to have more urosome spines (pp. 30–2). The same is true of the telson. In a sense, then, spines tend to replace hairs on these body parts.

Accessory flagellum

To illustrate the small, but significant, difference in the number of segments in the accessory flagellum, some samples were counted from the Plymouth area, and the results are given in Table II. The specimens are grouped in 2 mm. lengths, and the two subspecies compared. In each size group *salinus* shows an excess, which averages about 0·8, or nearly 1 segment more. The difference is perhaps better expressed as a ratio between the means, this being about 1·15:1. Thus young mature male *salinus* have an average excess of 0·6, and the largest of at least 1·0.

A similar contrast has been observed in samples from other parts of the British Isles. In *G. z. zaddachi* a total of seven segments is the usual maximum, while a total of nine is not rarely attained in large *salinus*.

TABLE II. NUMBER OF SEGMENTS IN MALE ACCESSORY FLAGELLUM

G. z. zaddachi

Size group (mm.)	Mean length (mm.)	No. of segments				Mean no.	Total specimens
		4	5	6	7		
20	19·7	—	—	1	2	6·7	3
18	18·1	—	—	5	5	6·5	10
16	15·9	—	2	4	4	6·2	10
14	13·7	—	9	23	—	5·7	32
12	12·2	7½	19	5½	—	4·9	32
10	10·0	16½	8	½	—	4·4	25
8	8·4	3	—	—	—	4·0	3
							115

G. z. salinus

Size group (mm.)	Mean length (mm.)	No. of segments						Mean no.	Total specimens
		4	5	6	7	8	9		
20	19·5	—	—	—	—	2	1	8·3	3
18	18·3	—	—	—	2	6	—	7·8	8
16	15·7	—	—	1	10	1	—	7·0	12
14	13·8	—	—	11	15	1	—	6·4	27
12	11·8	—	12	25	4	—	—	5·8	41
10	10·1	1	31½	6½	—	—	—	5·1	39
8	8·4	5½	8	1½	—	—	—	4·7	15
									145

N.B. Half-values are given when right and left sides are different, or when a segment is nearly but not completely divided.

Difference in the number of segments is reflected in difference in length, which can be made relative to another part of the body, and which is thus a more serviceable character. The accessory flagellum is conveniently compared with peduncle segment 2 (reference may be made to Fig. 5). In *salinus* the two are of about equal length at the onset of maturity, but when the animal is fully mature the flagellum is 25–35% longer (as shown by micrometer measurements). In the typical subspecies the flagellum is distinctly the shorter at onset of maturity, and increases only to 96–105%, or so, with age. At the start, in British brackish-water animals, it is some 75–85%, soon increasing to the region of 100%; but in four well-grown fresh-water males from Hamburg and Bremerhaven (E. W. Sexton Coll.) values fall between 59 and 80% only, while comparably short flagella were observed in a sample from Swinemünde, Prussia (Copenhagen Mus. Coll.). It is possible therefore that a greater contrast in this character difference may be found on the continent.

In females the contrast is very much less, at least in Britain. Those of *G. z. salinus* seldom have an accessory flagellum appreciably longer than peduncle segment 2.

Uropod 3 inner ramus

In British populations there is normally a visible difference in the relative length of the inner ramus of uropod 3, which tends to be longer in *salinus*. It is conveniently compared with the length of segment 1 of the outer ramus. In the data quoted, the uropods were mounted in chloral medium and measured with a micrometer in units of 1/75 mm. The standard end-points of the measurements are shown in Fig. 6 D. The length of the outer ramus of segment 1 gives an absolute length measurement which (unless the limb is regenerating) is a close index of the size of the animal: it averages 1/7·5 the body length (measured from head to apex of telson). The length of the inner ramus is expressed as a proportion of it.

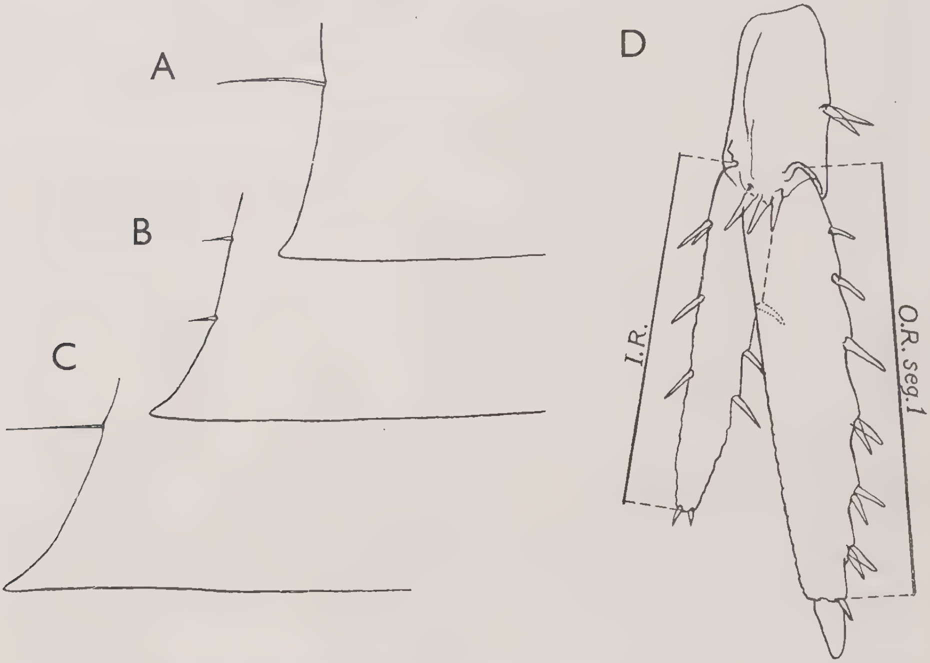

Fig. 6. Examples of the posterior distal angle of epimeron 3, right side, in (A) *Gammarus zaddachi zaddachi*, (B) *G. zaddachi salinus* and (C) *G. locusta sens.str.* (D) *G. zaddachi salinus*, male uropod 3, with setae omitted, showing the end-points of measurements on the inner ramus (*I.R.*) and the first segment of the outer ramus (*O.R.* seg. 1).

In Table III the total results for adult males from south-west Devon are compared. The *G. z. zaddachi* animals were taken from samples from the Rivers Tamar, Tavy, Plym, Erme, and their branches; the *salinus* animals from the Avon, and from the Tamar and its branches. Only animals in which the outer ramus segment 1 was at least 110 units (1·47 mm.) are included.

TABLE III. RELATIVE LENGTH OF UROPOD 3 INNER RAMUS. *G. ZADDACHI* FROM SOUTH-WEST DEVON

Ratio length of inner ramus to that of outer ramus segment 1

	0·66	0·67	0·68	0·69	0·70	0·71	0·72	0·73	0·74
G. z. zaddachi	2	3	9	3	9	13	16	14	15
G. z. salinus	—	—	—	—	—	—	—	—	—

	0·75	0·76	0·77	0·78	0·79	0·80	0·81	0·82	0·83
G. z. zaddachi	3	1	2	1	1	1	—	—	—
G. z. salinus	—	—	1	5	4	11	17	8	11

	0·84	0·85	0·86	0·87	0·88	0·89	0·90	0·91	0·92
G. z. zaddachi	—	—	—	—	—	—	—	—	—
G. z. salinus	10	5	6	4	4	6	—	1	—

	Total	Mean	S.D.
G. z. zaddachi	93	0·718	±0·0272
G. z. salinus	93	0·830	±0·0316

The mean for the typical form, 71·8%, compares with 83·0% for *salinus*. The overlap is small, and is smaller still when specimens of the same size are compared, as there is a tendency for the ratio to increase slightly with age.

If the data in Table III are split up according to localities, good uniformity in the component samples is shown. There is no significant difference in the localities involved in each set (Table IV).

TABLE IV. INNER RAMUS RATIOS

Localities for *G. z. zaddachi*	*n*	Mean	Localities for *G. z. salinus*	*n*	Mean
R. Tamar, St John's	25	0·723	R. Tamar, Weirquay	7	0·824
R. Plym	29	0·716	R. Tamar, Cargreen	26	0·831
R. Erme	22	0·710	R. Tamar, Tamerton Lake	21	0·829
Misc. (R. Tavy, Tamar, Yealm)	17	0·727	R. Tamar, Ernesettle	19	0·824
			R. Avon	20	0·836

Maturing males, represented in size groups 78–109 units, show a comparable difference, though, owing to the heterogony taking place at this stage, the ratio is somewhat lower in each, and the variation is greater (Table V).

TABLE V. INNER RAMUS RATIO IN MATURING MALES

	n	Mean	S.D.
G. z. zaddachi	28	0·700	±0·0367
G. z. salinus	56	0·808	±0·0465

The degree to which, after maturity, the ratio may alter with increased size is indicated by the figures in Table VI. There is a definite trend for a small increase which is not altogether negligible.

TABLE VI. INNER RAMUS RATIO AT DIFFERENT SIZES

Size group (length outer ramus segment 1 in 1/75 mm. units)	*G. z. zaddachi*		*G. z. salinus*	
	n	Mean	*n*	Mean
Over 200	1	(0·73)	—	—
160–199	17	0·728	14	0·842
135–159	29	0·729	28	0·836
110–134	46	0·709	51	0·825

Among other measurements on British *G. z. zaddachi* are the following. Ten specimens from the River Char at Charmouth, Dorset, all in the 135–159 group, give a mean of 0·726, conforming with the South Devon samples. A somewhat higher mean of 0·749 is given by a sample of 15 (of various sizes) from Appledore, North Devon. Too great stress is not laid on the exact values of the means, which may well vary a little in different areas: the significant fact is that an appreciable difference is maintained between *G. z. zaddachi* and *G. z. salinus*.

The contrast, however, may be appreciably less on the continent. From ten males of the fresh-water population of *G. z. zaddachi* (nine from Hamburg Wasserleitung and one from Bremerhaven), whose uropods were mounted by Mrs Sexton, the following results were obtained:

Size group	*n*	Mean ratio
160–199	4	0·794
135–159	2	0·802
110–134	1	0·76
96–109	3	0·758

I also observed that some of the specimens of *G. z. zaddachi* from Denmark (Copenhagen Mus. Coll., kindly lent by Dr K. Stephensen) appeared to have a longer inner ramus than is usual in British material. There is no evidence that *salinus* gives a comparably higher value.

Urosome dorsal spines

The pattern of the spine groups on the dorsal surface of the three urosome segments is usually given in descriptive works as a 'spine formula', in the form of the following example:

3 : 2 : 3
3 : 2 : 3
2 : 2 : 2

where the top row represents the number of spines in the left, centre, and right groups of segment 1, the second row those of segment 2, and the third of segment 3. The example given is that recognized as rather characteristic of *G. zaddachi* (e.g. Sexton, 1942, p. 600).

The above numbers are good central values for the species, but there is a marked variation in both directions for most of the groups. Even if full allowance is made for loss of spines through damage, there is frequently a difference between the numbers on the two sides of the body. As will be seen, the formula given above is virtually a minimum for *G. z. salinus*, and a maximum for *G. z. zaddachi*.

For *G. z. zaddachi* counts have been made on 81 males from the following localities: River Tavy, South Devon (8); River Plym, South Devon (47); River Char, Dorset (10); River Severn (16). The average values for the different groups tend to be similar in the four component samples, and there is no appreciable change with the size of the animal, so the total averages can be taken as representative. These are:

2·15 : 2·01 : 2·15
2·50 : 1·99 : 2·44
2·05 : 1·98 : 2·05

The centre groups of all three segments and the lateral groups of segment 3 have nearly a constant number of 2 spines, quite rarely 1 or 3. The lateral groups of segment 1 have usually 2, sometimes 3; and for segment 2 there are 2 or 3 about equally frequently: either may rarely have 1 or 4.

The total number of spines ranges from 13 to 23, 80% of individuals having 18 to 21. The mean value for the sample is 19·4.

By contrast, *G. z. salinus* shows a strong tendency to increased values, but individuals vary much. A sample of 20 from the River Avon, South Devon, gave the following averages:

3·1 : 2·3 : 3·15
3·05 : 2·1 : 3·4
2·4 : 2·0 : 2·5

Total spines: range 21–28, most frequently 22–25; mean value 24·0.

One of 16 from the Severn Estuary gave:

3·23 : 3·08 : 3·23
3·38 : 2·38 : 3·62
2·69 : 2·00 : 2·62

Total spines: range 20–34, most frequently 23–28; mean value 26·3.

The Severn population has the spines noticeably well developed, and the averages are probably higher than usual. The Avon sample appears to be more typical of *salinus* as a whole, judging from notes which have been made on other samples.

In *salinus* the central groups are usually not uniformly 2–2–2, as in the typical form, a constant value of 2 being found only for the third segment. The second segment centre group, though most often 2, is sometimes 3; while the anterior group is more frequently 3 and may be as high as 5. The lateral groups show a still greater average difference: segment 1 has most often 3, sometimes 4, rarely 2 or 5 (as against usually 2, sometimes 3); segment 2 has much the same, except 4 is more frequent (as against 2 or 3 equally frequent); segment 3 values of 2 and 3 about equally frequent (as against a nearly constant value of 2). The total number of spines ranges between 20 and 34 (compared with 13–23), but relatively low values, such as 22 and 24, are common. The mean of 24 compares with 19·4 in *G. z. zaddachi*.

This character difference appears to be shown equally in both sexes, and to hold for both British and continental material.

Presence of calceoli in the female

The peculiar organs known as calceoli, which occur on the more proximal segments of antenna 2 flagellum (see, for example, Sexton, 1942, p. 598, and pl. i, figs. 2, 3), are present in many *Gammarus* males. For example, they occur in the males of *G. locusta*, *G.* sp. (northern '*locusta*'), *G. setosus*, *G. wilkitzkii*, *G. zaddachi*, *G. duebeni* and *G. pulex*; but they are absent in *G. tigrinus* and *G. chevreuxi*. The presence of calceoli seems usually to be a male characteristic; though Sexton has not regarded it as such in *G. zaddachi*, and recently the writer has observed calceoli in females of *G. setosus* and *G. wilkitzkii* (probably a constant feature in these two species).

The position in *G. zaddachi* proves to be unusual, for calceoli may or may not be present in the female. The organs are, indeed, often developed in females of *G. zaddachi salinus*, though they may not begin to appear until after maturity; and they may be completely lacking, even in the largest and oldest individuals. On the other hand, in *G. z. zaddachi*, no females bearing calceoli have so far been observed. While this feature seems to merit further investigation, it is probably safe to say that there is a significant difference between the two subspecies in the tendency for the females to bear calceoli.

Habitat

The rather pronounced difference in the optimum environment and limits of range can be expressed quite satisfactorily in terms of salinity. Detailed discussion is deferred until the full ecological data have been presented. To summarize briefly, *G. z. salinus*, in Britain, inhabits brackish waters of various intermediate salinities with a general mean value of about 17 $^{0}/_{00}$. The middle reaches of estuaries which do not show too steep a salinity gradient provide habitats where the densest British populations have been found. It is here that the greatest range of salinity fluctuation in the estuary occurs, both diurnal, between high and low water, and periodic, between spring and neap tides; and it is here that the variety of the fauna is at a minimum. But daily fluctuation on its own is not an essential factor, as may be witnessed by the flourishing population towards the mouth of the River Severn. In Britain it is difficult to find brackish lagoons comparable with, for example, Frisches Haff, in Danzig Bay, and no British populations from a habitat of this kind have been observed. The limits of range have therefore to be defined in terms of estuarine conditions.

At the seaward limit of its range it persists so long as there is an appreciable lowering of salinity at high water. It seems not to tolerate a mean high-water salinity of more than 31 °/₀₀, even though the low-water value is much less. At the other end, it disappears when there is too much fresh-water influence at low water, that is when the mean low-water salinity is between 1 and 4 °/₀₀.

G. z. zaddachi has an optimum where the low-water salinity is quite fresh or below 1 °/₀₀, but where a marked rise of salinity occurs at high water. Its estuarine limit is roughly defined by a mean low-water salinity of 5 °/₀₀, with a mean high-water salinity of 10 to 15 °/₀₀. At the river end, it may penetrate for several hundred yards, or even miles, into permanent fresh water, but here, in most British rivers and streams, it fails to reproduce. On the other hand, in some areas (e.g. north Irish lakes, River Elbe) it is capable of breeding and flourishing in pure fresh-water environments. The species as a whole shows a marked preference for waters with good currents, and is clearly not so tolerant of stagnant water as is *G. chevreuxi* and *G. duebeni*.

The localities which provide conditions suitable for *G. z. salinus* (in Britain very largely limited to estuaries of rivers) are less numerous than for *G. z. zaddachi*. Nearly every river (and most streams flowing on to the shore) provides, at the head of its estuary (or near high-water mark at its inflow), a region in which *G. z. zaddachi* can exist. On the other hand, in the tidal zone of streams, or in the estuaries of some rivers, the mean salinity gradient may be too steep to provide living space for *salinus*. Under these conditions population samples show *G. locusta* giving place to *G. z. zaddachi* with a narrow zone of overlap in which the *Gammarus* population is sparse.

Constancy of character differences

The separation of the two subspecies, as described above, is justified on morphological grounds alone, since individuals can always be placed in one or other category. It is important, however, to be able to present confirmatory evidence from experimental data. This can be done. Laboratory observations will be described in necessary detail in a later section of this work, but some main results may be summarized at this stage. In one set of experiments, the effect has been tested of rearing *G. z. zaddachi* in salinities higher than those of its normal habitat, e.g. 14, 17·5, 24 °/₀₀, etc. If any of the character differences found between *G. z. salinus* and the typical subspecies are simply the direct effect of differences in the environment, it is in salinity differences that the major effects can only be sought, as indeed Sexton has strongly suggested. Even the mere difference between the equable laboratory environment and the fluctuating conditions of the natural habitat might alter characters. The results so far obtained show complete absence of such effects. The F_1 generation retains the same degree of hairiness, etc., possessed by its parents, even when reared at 24 °/oo salinity. Even an F_2 animal, reared to late immaturity in pure sea water, as were its parents, was found to retain characters diagnostic of its type. These results are consistent with the field observations that the two forms retain their type characters in the zone where their populations overlap; and that within the range of each of them there is no evident gradation of lesser variations from the fresher to the salter end. It is also noteworthy that *G. z. salinus* from the Baltic coast of Germany, living at more or less constant salinities of 7–8 °/oo, or less, shares the same type characters as those from British estuaries with salinity fluctuating around 17 °/oo, and laboratory-reared animals kept at a constant salinity of 27 °/oo. It is clear that phenotypic variation due to salinity differences can at best be of very limited extent. Results obtained by Höfken (1937) with *G. zaddachi* from the West Baltic had already pointed to this conclusion.

Intersterility

A further, and most significant, piece of experimental evidence comes from breeding experiments which were at first designed to test the genetic relations of the two types by crossing. Results obtained in 1938 have been amply confirmed by a more extensive and detailed experiment carried out in 1946. It is conclusively shown that, under conditions in which both subspecies breed freely and normally (e.g. in 14 °/oo salinity in bowls), they are incapable of producing fertile eggs with one another, whichever way the cross is made. They also mate (i.e. form pairs) less readily with each other than with their own kind. This (*a*) shows that there is important genetic difference between the two types, to which their character differences must be attributed, at least in some measure; (*b*) explains completely how it comes about that the populations remain distinguishable in nature even in the zone where individuals of both mix freely.

The question immediately arises whether sterility may not be prevalent among different populations of the same subspecies, in view particularly of the isolation which occurs between populations of neighbouring watersheds. So far as present information goes, there is no evidence for this, though tests with animals from widely separated areas have yet to be made. For instance, *G. z. salinus* from the River Avon, South Devon, breed normally with those from the River Tamar. *G. z. zaddachi* from Weymouth, Dorset, proved fertile with others from the River Erme and River Yealm, South Devon; while others of this subspecies from several South Devon localities have been bred together.

Genotypic versus phenotypic variation

The results obtained up to now in the study of variation in *Gammarus zaddachi* thus contain an element of surprise. From the evidence brought forward in existing literature, it was at least to be expected that evidence of environmental variation would be quickly forthcoming, and that no taxonomic division of the species would prove possible. Yet positive proof has been found for *genetical differentiation*, in that there are (at least) two main intersterile subdivisions of the species; whereas no positive evidence for *phenotypic differentiation* can yet be given.

It seems that more attention must be given to the possibility of different genetic types within the species, and that where differences are found in the characters of two populations these are not necessarily, or even probably, phenotypic, even if they show correlation with some definable environmental factor. In Britain two main well-differentiated genetic types have been demonstrated. Elsewhere there may be more than two of such 'major types', equally incapable of crossing with the typical subspecies and with *salinus*. If another such form exists, there is little chance that it would be absolutely distinguishable morphologically, and much closer statistical study might be necessary to recognize it. If it happened to bridge the gap between *G. z. zaddachi* and *salinus* an impression of continuous variation might be obtained; or if it closely overlapped one of them, it might escape detection until tested by breeding.

It would be useless to try completely to reconcile the picture presented by Sexton with the present viewpoint, until the former is supported by the necessary experimental observations. However, it is scarcely reasonable to suppose that conditions in the River Elbe, for example, are essentially different from those in British rivers. It has yet to be proved, that, if re-examined in the light of the character differences which hold good for British populations, two major types cannot equally well be separated in Germany, even if the variation within each is somewhat greater. The mystery of the 'intermediates' Sexton records is largely resolved by the discovery that these include *G. z. zaddachi* with somewhat less dense hairs than in the Hamburg 'fresh-water' population, especially on antenna 1 flagellum, but which characterize the bulk of the *G. z. zaddachi* population of south-west England.[1] Until proved to the contrary it can only be assumed that the 'fresh-water' form plus most of the 'intermediates' of Sexton fall within the typical subspecies, while the 'brackish water' form includes *salinus*.

The alternative possibility that the *salinus* types completely intergrade with the typical form towards the more eastern part of the species' range, whereas westwards, in Britain, they have become quite separate and genetically isolated, provides an attractive solution to the problem. Though improbable, this may yet be partially true and would not be without parallel among other animals. But this conclusion would be of too great theoretical interest to be accepted so long as the crucial experimental data for the continental populations is lacking.

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[1] According to Mrs Sexton, who has recently been kind enough to look over some of my material, a large proportion of British *G. z. zaddachi* would be classed, in her original terminology, as 'fresh-water intermediates', a few as the 'fresh-water' form, or very nearly so, and others as grading between the two.

Taxonomic status

The two major genetic types into which *G. zaddachi* has been divided (without prejudice to the fact that others may exist or even that further subdivision may be necessary), behave, for all practical purposes, as two distinct species. Ecologically they can profitably be treated as such. The reasons for not giving them specific rank are briefly as follows:

(1) Though separable on good visible differences in the development of spines and hairs, supported by average differences in various other respects, the two forms are identical, or very closely similar, in structures which normally show diagnostic specific characters, particularly the gnathopods, coxal plates, relative size of antennal segments, etc. Also both have the diagnostic pattern of hair tufts associated with *G. zaddachi*. Taxonomically, therefore, they are closer than other species of the genus are to each other. If they were made separate species, a dangerous precedent might be set for wholesale splitting in other species.

(2) Some uncertainty still remains on the relation between the *salinus* and typical forms in the eastern part of the range of *zaddachi*. Until this matter is clearer, it is advisable to proceed cautiously.†

Separation from related species

G. z. salinus has been liable to confusion with *G. locusta* (*sens.str.*), with which it mixes near the mouths of estuaries. They are very easily separated in mixed samples, however, by the longer accessory flagellum of *locusta*, its relatively short segments 2+3 of antenna 1 peduncle, which has very sparse hairs, the more spreading and less graded hair-tufts of antenna 2, the more greatly elevated urosome segments, the deeper and more rectangular ventral half of coxal plate 4, the long uropod 3 inner ramus, etc. In adult males the diagnostic gnathopod 2 hands are alone sufficient. In adult females the hand of gnathopod 2 of *locusta* is notably elongate, easily more than twice as long as broad (except in the youngest individuals), whereas in *zaddachi* it is easily less than twice. Immatures of all sizes can be readily separated, if examined when freshly killed, by the presence of reddish pigment spots on the peraeon segments of *locusta* (absent in *zaddachi*); otherwise the more numerous hairs on antenna 1 peduncle ventrally in *zaddachi* become evident at least by the time the immature are half-grown.

G. z. zaddachi is further distinguished from *locusta* by the abundance of hairs on the hinder parts of the body (though the hairs on the distal segments of peraeopod 7 are usually longer and more numerous in *locusta* than in *G. z. salinus*). The habitats, however, are usually well separated.

It is, however, to *G. duebeni* that *G. z. zaddachi* bears the closest superficial resemblance, as older determinations often bear witness. Their habitats are

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† This uncertainty has been largely removed by Segerstråle (pp. 236–40), who, all the same, independently decided that *zaddachi* should not be split into separate species.

liable to overlap, and mixed populations are collected in some localities. Adult males are at once separable on the form of the gnathopods: in *duebeni* the hand of gnathopod 2 is scarcely longer than that of gnathopod 1, while the median palmar spine and the angle spines of gnathopod 2 form a continuous row (Fig. 7). All sizes of *duebeni*, particularly the immature and younger adults, are separable at once by the shape of the basal segment of peraeopods 6 and 7—the posterior distal angle protruding and lacking spines, though this feature tends to be less evident in larger adults. In *duebeni*, moreover, the setation of antenna 1 peduncle is sparser, that of antenna 2 more concentrated in brush-like tufts; coxal plate 4 has a more rounded and U-shaped ventral

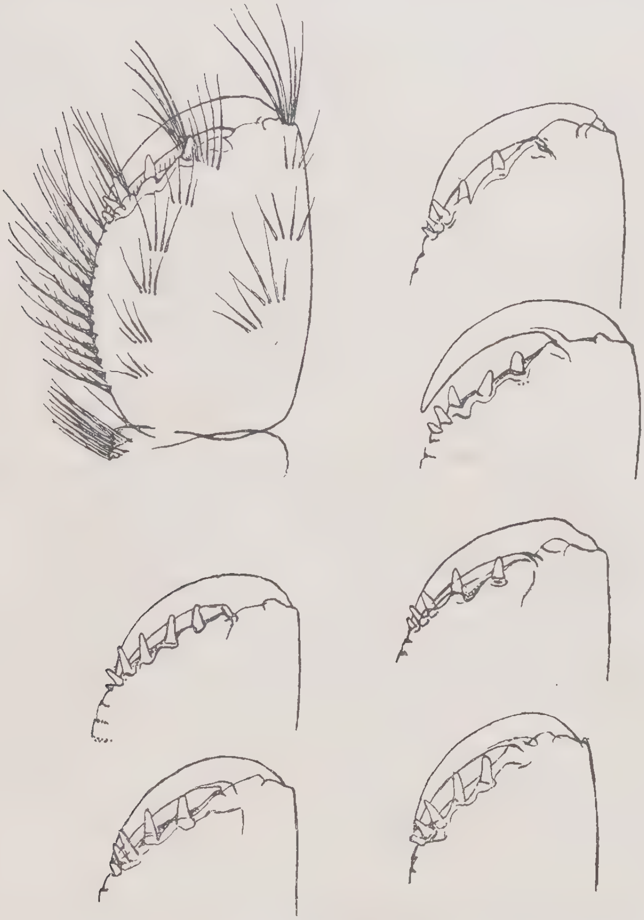

Fig. 7. *Gammarus duebeni*, from Chelson ditches, near Plymouth, male gnathopod 2 hand. One figured complete, and the distal part of six others with setae omitted, to show the arrangement and form of the palmar spines.

expansion; the angles of the epimera are more nearly right angles; and the whole body is distinctly less slender. Immatures can be satisfactorily distinguished, to the smallest sizes, on the strength of the produced distal angle of peraeopod 7 basal segment.

G. chevreuxi, which is liable to occur in company with *G. z. zaddachi*, having a very similar salinity tolerance, is readily distinguished by its smaller size, the pronounced dense curled hairs of the male antenna 2, and the sparser, less graded, antennal hairs of females and immature, and the sparsity of hairs on the hinder part of the body. The shorter segment 2 of antenna 1 peduncle is also quite evident.

Material examined

Samples marked by an asterisk will be reported on in greater detail subsequently, when population analyses are discussed. Most of G. I. Crawford's collections (up to 1937), which have been kept at the Plymouth Laboratory, refer to records published by Crawford (1936, 1937).

Abbreviations: E. W. S., Mrs E. W. Sexton; G. I. C., G. I. Crawford; A. D. H., Prof. A. D. Hobson; coll., collected by; Coll., collection.

G. Z. ZADDACHI

England and Wales. WEST CORNWALL: Gannel Estuary, 20. xi. 37, creek at head of estuary, in saltings zone, mated pairs under stones. EAST CORNWALL: Camel Estuary, 5. v. 35, coll. G. I. C., Egloshayle, in river, with *G. chevreuxi*; 28. i. 40, Trewornan, ♀ in salting pool with *G. chevreuxi*. EAST CORNWALL and SOUTH DEVON: Estuaries of Rivers Tamar, Lynher, and Tavy. River Tamar, main channel; various samples* at different times, from the limit of estuarine influence at Weir Head downstream to North Hooe, exceptionally at Thorn Point; abundant at Weir Head, 3. vii. 38, but not breeding, and even present in the river above the Weir where the water is permanently fresh; from about Calstock downwards overlapping with *G. z. salinus*. Whitsame Creek, 12. vii. 35, and Kingsmill Lake, 2. viii. 35, coll. G. I. C. Tamerton Lake, 24. xi. 37, 28. iv. 38, 2. v. 38*; in upper half of main channel of creek, mixing with *G. chevreuxi*, and towards middle overlapping *G. z. salinus*. River Tavy, 19. v. 38, 19. vi. 38*; in main channel from Maristow Ford up to extreme limit of tidal influence, abundant, mixing with *G. chevreuxi*; Maristow and Lopwell areas, main channel and adjacent brackish creeks, 3. vii. 35, coll. G. I. C. River Tavy, Gnatham, 1937, E. W. S. Coll., some large adults in a pool at about extreme H.W. level; Gnatham Creek, 28. vii. 38*, in stream flowing into tidal zone of estuary, mixing with *G. chevreuxi* in tidal zone, and alone in fresh water above tidal influence. St John's Lake, at extreme upper end, in tributary stream by the road bridge, 18. xii. 37, 5. v. 38, 28. iii. 40, 12. xi. 46*, plentiful when adequate cover available, mixing with *G. chevreuxi*; sparingly further down channel in estuarine zone, meeting *G. locusta*. River Lynher: near St Germans, 25. vi. 38, coll. E. Percival, several, with two *G. duebeni*; Sheviock Wood, south end, 18. ii. 38, a number in stomach of a sea-trout, coll. P. H. T. Hartley. SOUTH DEVON: River Plym: in main channel at upper end of estuary, 2. vi. 38, 1. viii. 38*, from extreme upper part of Laira Lake to the river above Marsh Mills, numerous, though water milky with China Clay, mixing with *G. chevreuxi* and overlapping *G. z. salinus*. River Yealm, Cofflete Creek, at head of creek near Spriddlestone, 19. xi. 37, 3. vi. 46*, plentiful, penetrating into fresh water and mixing with *G. pulex*. River Erme, 1. i. 38, 18. ii. 39*, in main channel opposite Holbeton and in three stations down the estuary, overlapping *G. z. salinus*; also in brackish ditch behind an embankment. River Avon, 16. v. 38, 14. vi. 38, 8. i. 39, 14. v. 46*, in main channel from about half a mile below Aveton Gifford up to near limit of estuarine influence, abundant, overlapping *G. z. salinus*. Kingsbridge Estuary, Blank's Mill Creek, 22. i. 39*, in three stations, overlapping *G. z. salinus* in middle of creek, and *G. pulex* in fresh water of stream above tidal influence. Dawlish, 21. vii. 35, coll. G. I. C., in Copenhagen Mus. Coll., a number of dwarfed adults, breeding. River Exe: 'Exeter', R. Elmhirst Coll., 6 ♂♂ and 1 ♀; Countess Weir, 21. vii. 35, coll. G. I. C., several in main stream, 3 ♂♂ in tidal ditch; Powderham, brackish pond, 21. vii. 35, coll. G. I. C., numerous, mixing with *G. duebeni*; Topsham, tidal zone of estuary, 24. x. 38*, several adults, overlapping *G. locusta* (*G. z. salinus* absent). River Axe, 21. xi. 38*, in main channel above Axmouth, overlapping *G. z. salinus*. NORTH DEVON: Torridge Estuary, 14. iii. 38, in brackish ditch near Appledore, large sample. Taw Estuary, Caen River, coll. G. I. C., 3 specs. DORSET: River Char, 21. xi. 38*, in river just above its fall over the beach, large adults. The Fleet, 27. iii. 38, in brackish ditch near Langton Herring. River Wey and Radipole Lake, 2–10. ix. 38*, in several stations, plentiful, though of small average size, in open water and in ditches, crowding amongst tubes of *Mercierella enigmatica* and at roots of *Phragmites*. Lodmoor, Weymouth, ditches near sea sluice, iv. 28, sample of large adults, 26. xii. 37, 14. xi. 37, sparingly. HANTS: River Test, Totton Br., 7. xii. 35, coll. G. I. C., in British Mus. Coll. [1936. 2. 12. 95–99]. SEVERN ESTUARY: In various samples from the upper reaches of the main estuary, coll. R. Bassindale, as reported in the 'Studies on the Biology of the Bristol Channel' series, nos. IV, VII, VIII and XI (Bassindale, 1941, 1942*a*, 1942*b*, 1943), recorded as '*zaddachi*, typical variety, Spooner (*in lit.*)', corrected to 'Form C Sexton';[1] in main channel and tidal zone of estuary from Aust (summer) or Sharpness (winter) to Ashleworth Ferry, also at Kilve where a tributary fresh-water stream flows over the tidal zone; overlapping *G. z. salinus* at Sharpness (summer) and from Aust to Sharpness (winter), while above Epney showing signs of inhibited growth and development, especially in winter. ESSEX: Benfleet, 8. iii. 36, in two places, coll. G. I. C. [British Mus. Coll., 1938. 2. 16. 52–59]. Leigh-on-Sea, 28. vi. 36, coll. G. I. C. [British Mus. Coll., do.]. NORFOLK: Stiffkey, 29. ix. 35, coll. G. I. C. [British Mus. Coll., 1936. 2. 12. 95–99]. DURHAM and NORTH-EAST YORKS: River Tees, Tees Survey collections (Alexander *et al.*, 1935), various samples from sections I, II, III, IV and VIII, in main channel or tidal zone. See pp. 46, 51. CARMARTHENSHIRE: River Towy, 25. viii. 35, coll. G. I. C., 'open stream through salting among Enteromorpha', 9 ♂♂, 2 ♀♀, 8 imm., 'above a sluice among grass', 10 ♂♂, 9 ♀♀, 15 imm. MERIONETHSHIRE: Aberdovey, at head of estuary, coll. E. E. Watkin, several ♂♂. ANGLESEY: Lake Maltreath, brackish water, 27. iii. 40, coll. J. B. Cragg, 6 ♂♂, 1 ♀. ISLE OF MAN: Castletown, Silver Burn, 7. ix. 38, coll. G. I. C., near mouth of fresh-water stream, flowing into the sea, in three stations, dwarfed. WESTMORLAND: River Gilpin, Sampool Br., 16. v. 38, coll. P. H. T. Hartley, 7 ♂♂, 6 ♀♀, 12 imm., average size small.

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[1] The correction in Bassindale (1942*b*, p. 314), which was added when the writer was away on war service, is now seen to have been superfluous. 'Typical variety' was the provisional name given to *G. z. zaddachi*; and 'saline variety' to *G. z. salinus*, which in the Severn can be incompletely divided into two forms, A and B (see p. 42). The statement that intermediate forms occur between Forms A and C (i.e. between the two subspecies) was incorrect.

Scotland. FIRTH OF TAY: River Tay, Tees Survey collections (Alexander *et al.*, 1935), identified from sections I, II, III, IV, VI, VIII, IX, X (see pp. 47–8, 52), small-sized from higher sections where salinity very low or mainly fresh water, in the two lowest Sections overlapping *G. z. salinus*. AYRSHIRE: Fairlie Sands, 7. vi. 40, coll. R. Elmhirst, in stream flowing into tidal zone of shore, overlapping *G. duebeni* at the fresh-water end, and *G. z. salinus* at the seaward end of its range (see Scottish Marine Biol. Assoc., *Annual Report*, 1942–3, pp. 11–12). ARGYLLSHIRE: Oban district, coll. H. P. Moon: Gylen Castle, 1. viii. 39, 'stream flowing over beach, just above *Enteromorpha* zone', 9 imm., with *G. duebeni*; Slatroch Bay, 12. viii. 39, 'stream across shore, about middle of bay, amongst *Enteromorpha*, associated with ephemerid *Baetis*', 2 ♂♂, 19 imm. INNER HEBRIDES: Skye, Kyleachin, 31. vii. 33, coll. R. Elmhirst, 'in shallow stagnant inlet of sea', ♂♂, ♀♀, imm., various sizes; 23. viii. 39, coll. H. P. Moon, 'point where stream flows over beach, and into *Enteromorpha* zone', 7 imm., in both samples mixed with *G. duebeni*. Isle of Muck, Port Mor, A. D. H. Coll., in fresh-water stream on shore, 29. vii. 38, 3 ♂♂, 1 imm. South Rona, vii and viii. 37, A. D. H. Coll., in three streams flowing over the shore, in tidal zone but not above mean H.W. (see Beadle & Cragg, 1940, as *zaddachi* 'hairy' variety), mostly small sizes. Raasay, viii. 37, A. D. H. Coll., in stream flowing over shore, above H.W., small ♀ and imm.; Oskaig Salt Marsh, 2 ♂♂, 6 imm., with *G. duebeni*. Mull, Kilbrenan Waterfall, 12. viii. 39, coll. H. P. Moon, 'tidal pool at foot of waterfall, *Pelvetia* zone', 2 young ♂♂, 23 imm.; *Enteromorpha* zone, 1 young ♂, 3 imm. OUTER HEBRIDES: South Uist, 1. viii. 32, R. Elmhirst Coll., Loch Bee, several, mostly males, not fully mature and dwarfed. North Uist, R. Elmhirst Coll., 18. vii. 33, Loch Obisary, brackish, several small-sized adults; 24. vii. 33, Sollas, stream from Loch Sandary, 1 imm.; 28. vii. 33, Loch an Sticar, adults and imm. Harris, near Tarbert, coll. H. P. Moon, 22. viii. 39, Glen Lingadale Burn, *Enteromorpha* zone, 10 ♂♂, 3 ♀♀ (breeding), 3 imm.; 20. viii. 39, Laxadale River, *Enteromorpha* zone, 17 ♂♂, mostly young, 24 young ♀♀ and imm. ORKNEYS: R. Elmhirst Coll., 'W. of Douglas Hill, upstream, amongst green alga and stonefly larvae, fresh water', 8 imm., including 2 developing ♂ characters.

Ireland. SOUTH KERRY: Kenmare, 23. vii. 38, coll. G. I. C., small brackish stream, 2 ♂♂, 1 ♀ (with one *G. z. salinus*). Glenbehy, 21. vii. 38, coll. G. I. C., brackish ditch, among *Fucus*, 6 ♂♂, 1 imm., in *Enteromorpha*, a number of smaller sizes (with *G. duebeni*). DUBLIN: River Liffey, at Kingsbridge, 17. vii. 38, coll. G. I. C., just below limit of tidal influence, 5 ♂♂, 16 ♀♀ and imm. (with *G. duebeni*). COUNTY DOWN: The Kinnegar, Holywood, coll. R. Macdonald, 'from a large drain inside the embankment', 6 ♂♂, 4 ♀♀, 10 imm., of very small size (E. W. S. Coll.); ♂ and ♀, 12. i. 36, same locality and captor (Copenhagen Mus. Coll.).

Belgium. Schelde Estuary, below Antwerp: Lillo, 'stream along road from Stabroeck', 15. v. 36, 4 ♂♂; Liefkenshoeck, 15. v. 36, 4 ♂♂, 9 ♀♀, 2 imm.; Copenhagen Mus. Coll. (ex Brussels Mus. Coll.).

Germany. RIVER ELBE: Hamburg Wasserleitung (conduits connected with former water supply), E. W. S. Coll., series of mounted parts of three males, and mounts of uropod 3 of six others, typical 'fresh-water' form, *teste* E. W. S. RIVER WESER: Bremerhaven, 12. v. 94, E. W. S. Coll., series of mounted parts of large ♂, 'fresh-water' form; 10. xi. 12, R. Elmhirst Coll. (*ex* E. W. S. Coll.), large ♂. (Examples of original material described by Sexton, 1912, 1942.) PRUSSIA: Swinemünde, 5 ♂♂, Copenhagen Mus. Coll. (from Prof. A. Schellenberg, Zool. Mus. Berlin), '*Gammarus locusta* f. *zaddachi*, typische form: A. Schellenberg *det.*' E. PRUSSIA: Danzig, Messina See, brackish water, ♂ and ♀, Copenhagen Mus. Coll. (R. Lucks, Marienburg, *col. et ded.*).

Denmark. Samples from Copenhagen Mus. Coll. WEST JUTLAND: Aagab (Holmsland), Ringköbing Fjord, coll. K. O. Leith, 7. vii. 42, one smallish ♂. Vondaa, between Heager and Kloster, coll. K. O. Leith, 27. vii. 42, 8 ♂♂, 7 ♀♀, 2 imm., breeding, abnormally dwarfed. SOUTH-WEST JUTLAND: Maade, 3 km. east of Esbjerg, 24. iv. 43, coll. E. Pedersen and K. O. Leith, ♀ and imm. NORTH-EAST JUTLAND: Randersfjord, Uggelhuse, near Bridden Thor, 19. v. 17, 1 imm. NORTH-WEST ZEALAND: Lammefjordssöen, to 3 m., 3. v. 23, 1 ♂ (Dansk. Biol. Sta. *ded.*).

G. Z. SALINUS

England and Wales. EAST CORNWALL and SOUTH DEVON: Estuary of River Tamar, and its tributaries River Lynher and River Tavy. River Tamar, main channel, various samples* from Saltash upwards to Calstock, overlapping *G. locusta* from Saltash to Cargreen (winter) or from Junction of Tavy to above Weirquay (summer), and at the upper end of its range overlapping *G. z. zaddachi* from near Weirquay upwards (winter) or from near North Hooe upwards (summer); absent from St John's Lake. Tamerton Lake,

28. iv. 38, 2. v. 38*, in main channel, overlapping *G. locusta*, *G. z. zaddachi* and *G. chevreuxi*. River Lynher, Sconner Creek, coll. G. I. C., 6. vi. 35, young ♂ and imm. River Tavy, 19. v. 38, 28. vii. 38, from junction with the Tamar to Maristow Ford, in open part of estuary, overlapping *G. locusta* and *G. z. zaddachi*. SOUTH DEVON: River Plym, 2 and 28. vi. 38, 17. i. 46, in main channel and tidal zone, from near south end of Laira Lake to below Marsh Mills road bridge, plentiful, overlapping *G. locusta*, *G. z. zaddachi* and *G. chevreuxi*; Chelson Sluice, 23. xi. 45, 2 ♀♀. River Yealm, in estuary near Steerpoint station, iv. 40, overlapping *G. locusta* (apparently absent Cofflete Creek). River Erme, 1. i. 38, 18. ii. 39, 5. iii. 39, from near estuary mouth to just below Holbeton, in main channel and tidal zone, plentiful, overlapping *G. locusta* and *G. z. zaddachi*. River Avon, 16. v. 38, 16. vi. 38, 8. i. 39, 14. v. 46, in main channel and tidal zone from near Bantham to a little below Aveton Gifford, abundant, especially in clusters of fucoid algae, as usual overlapping *G. locusta* in one direction and *G. z. zaddachi* in the other, with a long stretch of 'pure' population in the middle of its range. Kingsbridge Estuary, Blank's Mill creek, 22. i. 39, in channel and tidal zone. River Axe, 21. xi. 38, above Axmouth, overlapping *G. z. zaddachi*. DORSET: River Frome, Wareham, coll. G. I. C., 2. ix. 35, 2 imm. SEVERN ESTUARY: In various samples from Bristol Channel coast and Severn Estuary, coll. R. Bassindale (see references given on p. 39 and the attached footnote), from at least Blue Anchor (winter) and Kilve (summer) upwards to Sharpness; the population tending to be dimorphic, the recorded 'Variety A' agreeing with *G. z. salinus* from other estuaries, while the more abundant 'Variety B', distinguished by its small eyes, and its unusually long hairs and spines, has been observed only from this estuary; the two varieties not always completely separable, and occurring throughout the range of the subspecies; occurrences correctly reported in Bassindale (1941); as elsewhere, overlapping *G. z. locusta* at the seaward end of its range (Blue Anchor to Weston) and *G. z. zaddachi* at the other end (Aust to Sharpness). LINCS: River Welland, near Holbeach, main dyke running into the river near Holbeach, 20. vii. 39, coll. M. L. Rothschild, 2 ♂♂, 2 imm. NORTHUMBERLAND: Blyth, 'ditch from saltpans', 4. vii. 34, A. D. H. Coll., 3 ♀♀, breeding, with *G. locusta*. Wansbeck, 9. iv. 35, A. D. H. Coll., 'below railway bridge, among *Fucus* in stream', 9 ♂♂, 10 ♀♀, 3 imm.

Scotland. AYRSHIRE: Fairlie Sands, 7. vi. 40, coll. R. Elmhirst, in stream flowing over tidal zone of shore, overlapping *G. z. zaddachi* (see Scottish Marine Biol. Assoc., *Annual Report*, 1942–3, pp. 11–12). CLYDE ISLES: Cumbrae, east of Keppel Pier, near Lion Rock, shore near L.W., 16. ii. 43, 2 large ♂♂. ARGYLLSHIRE: Clachan Strand, 2. vi. 35, 'under weed', A. D. H. Coll., young ♂ (with *G. locusta* and *M. marinus*).

Ireland. SOUTH KERRY: Kenmare, 23. vii. 38, coll. G. I. C., small brackish stream, 1 ♂ (with *G. z. zaddachi*).

Germany. RIVER WESER: Bremerhaven, Alter Hafen, Dec. 1911, Herr Klie; E. W. S. Coll., series of mounted parts of young adult, figured by Sexton, 1912, and a few immature specimens (types).

Denmark. SOUTH ZEALAND: Stege Nor, opposite Kirkegrund, 25. vii. 29, 1 young ♂, Copenhagen Mus. Coll. (E. Poulsen *ded.*).

The following examples, originally identified with *salinus*, are separable on characters of the antenna 1 peduncle (Fig. 5 F), and by the somewhat more angularly elevated urosome segments. Apart from their relatively small size, they approach very close to the northern *G.* '*locusta*'.† Amongst them is a female specimen, from Raasay, which is unusually large for a British *zaddachi* (21 mm.). Amongst characters shared with *salinus* are all those in which the latter differs from *zaddachi* typical. It is possible that the Cumbrae specimens recorded above should also be included in this category.

Scotland. FIRTH OF TAY: Tees Survey collections (Alexander *et al.*, 1935), in sections IX and X of the estuary (see pp. 48, 52). INNER HEBRIDES: South Rona, vii and viii. 37, A. D. H. Coll., in stream flowing over shore, well below H.W., ♂ and imm. (Beadle & Cragg, 1940, as '*zaddachi*, hairless var.'). Raasay, vii and viii. 37, A. D. H. Coll., in stream flowing over shore between tide-marks, 6 ♂♂, 1 ♀, 11 imm.

Germany. EAST PRUSSIA: Rauschen, Königsberg, series of mounted parts of adult ♂ and ♀, E. W. S. Coll. (see Sexton, 1912, 1913).

REVISION OF PUBLISHED IDENTIFICATIONS

Fauna of Tamar and Lynher (Percival, 1929)

The faunistic survey of the Tamar estuary, and its branch the Lynher, carried out by Percival in 1928, has been frequently quoted in comparisons with other estuaries. It is necessary that his statements concerning the *Gammarus* fauna (Percival, 1929, pp. 92–3, 103) should be corrected in the light of present knowledge.

A small reference collection was left by Percival in the Plymouth Laboratory. This, unfortunately, was unknown to Crawford (1936, 1937), and overlooked by Sexton (1942).

Percival did not submit his Gammarids to a specialist for confirmation. This might have seemed unnecessary, as at the time the choice of species apparently lay simply between *G. locusta* and *G. duebeni*. As a result *G. zaddachi* was completely overlooked, and *G. chevreuxi* (at the time known only from Chelson Meadows ditches) missed.

G. locusta. Though no specimens were preserved, it is quite clear, as Crawford suspected, that Percival included *G. zaddachi salinus* in this category.

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† Both are now to be included in Segerstråle's third subspecies of *zaddachi* (pp. 223 *et seq*). This form would appear to replace *salinus* in north Scotland, and so raises a new problem.

The upper limit at Morwell Rocks is in fact rather higher than the point reached by *salinus* in June 1938, but might well represent the extreme upper limit of that form in a dry summer. The true upper limits of *locusta* are found to be at the bend above Weirquay in an average summer, and at Cargreen in the winter. This applies to the region of low water: the species penetrates a little higher in the upper half of the tidal zone.

G. duebeni. This species is not a normal inhabitant of the main stream of the estuary, but is virtually confined to backwaters and side channels, e.g. pools near high-water level fed by fresh-water seepage, salting pools, ditches separated from the river by sluices, etc. The form recorded as '*duebeni*' by Percival in the Tamar 'from Cothele Woods to Weir Head' is really *G. z. zaddachi.* Its summer range is thus quite accurately described, and, as Percival noted, it swarms amongst moss at Weir Head. Similarly this is the form which frequents the Lynher 'from Sheviock Wood to Tideford', as is proved by a preserved sample, labelled '*G. duebeni*, R. Lynher, near St Germans, 25. vi. 28'. This sample contained 8 ♂♂, 5 ♀♀ and 1 imm. *G. z. zaddachi*, as well as one large ♂ and one small ♀ *G. duebeni.*

No comment is necessary on the range of *Marinogammarus marinus*, there being good agreement with later observations. It should be emphasized that the population of this species is concentrated in the region of high-water neaps, and usually the species is quite absent from the low-water region, unless the gradient of the intertidal zone is steep.

Amongst other crustaceans in Percival's samples which have been examined are the following:

Sphaeroma serratum F. Wyvlescombe Lake, River Lynher, 22. viii. 28, confirmed correct.

Sphaeroma rugicauda Leach. River Tiddy and Marsh, 25. vi. 28. 5 ♂♂, 5 ♀♀, confirmed correct.

Jassa falcata (Montagu). R. Lynher, 20. vii. 28, 2 ♂♂ of form with large gnathopod hands. Hamoaze, 19. vii. 28, on no. 15 Buoy, 2 ♂♂, 2 ♀♀ (recorded as *Podocerus odontonyx* Sars).

Cyathura carinata (Kröyer). As Crawford (1936, p. 37) rightly suspected, Percival's records for *Anthura gracilis* Montagu really refer to this species. Specimens from Rat Island, 30. viii. 28, were preserved.

Collections by G. I. Crawford and others

Subsequent to the discovery of *G. zaddachi* in Britain, estuarine collections of gammarids have been given deserved critical attention. Recent records from the south-west, published by Serventy (1935), Crawford (1936, 1937), Milne (1940), Spooner and Moore (1940), require no further qualifications, except in one respect. In the various records of *G. zaddachi* distinction has to be drawn between the two subspecies.

Serventy (1935) first recorded the occurrence of the species in the Tamar, from collections made at Pentillie Quay, Whitsam, and at a point one mile below Calstock in March 1934. Two tubes of Serventy's specimens have been examined: one labelled Pentillie Quay, and the other without locality label. Both contain *G. z. salinus*, the former 6 ♂♂, 5 ♀♀ and 7 imm., the latter many of various sizes.

Mr G. I. Crawford added much to our knowledge of the distribution of Amphipoda in the west. Most of his preserved collections remain at the Plymouth Laboratory, and it has been possible to re-examine nearly all the *G. zaddachi* he records (Crawford, 1936, p. 102; 1937, pp. 650–60).

From Rivers Tavy, Tamar and Lynher (p. 650), the following records refer to *G. z. salinus*:

Rat Island, low water, 31. v. 35, 2 imm. amongst *G. locusta*.

Neal (or Neille) Point, 2. viii. 35, on buoy, a number, mostly ♀♀ and imm.

Crosspark Wood, 3. ix. 35, among *Obelaria gelatinosa* at low water, small ♀ and imm.

Lynher, Sconner Creek, 6. vi. 35, west bank among Fucus, young ♂ and several imm.

The following refer to *G. z. zaddachi*:

St Budeaux, open creek. Kingsmill Lake, creek above sluice. Whitsam and Haye creeks. All samples from the River Tavy in the region of Blaxton, Mt Jessop and Lopwell, in main channel and creeks.

The *G. zaddachi* recorded from the upper estuarine zone of the River Exe (p .652), River Taw (p. 654), River Camel (p. 654) and River Towy (p. 655), are all *G. z. zaddachi*. The sample from a pond on the Powderham Estate, River Exe region, contained many *G. duebeni* mixed with the *zaddachi*. Two immatures from the River Frome at Wareham, Dorset (p. 102), are *G. z. salinus*.

In his investigation of the fauna of buoys in the seaward part of the Tamar estuary, Milne (1940) again found *G. zaddachi* present on Neal Point Buoy, and his specimens proved to be *G. z. salinus*.

Tees Survey Material

The first comprehensive survey of a British Estuary was carried out on the River Tees, supplemented by observations on the River Tay. The results were published in three parts (Water Pollution Research, *Technical Papers*, no. 2, 1931; no. 5, 1935; no. 6, 1937). In the analysis of fauna of the estuarine zone in Part II (Alexander *et al.*, 1935, p. 44 onwards), five species of *Gammarus sens.lat.* are recognized from the two rivers (p. 55). At the time of the survey, however, the status and distinguishing features of *G. zaddachi* were still not widely appreciated, and the species into which *Marinogammarus marinus* auctt. has recently been separated were still unknown.

Fortunately representative samples of the fauna were deposited at the Plymouth Laboratory, and it has been possible to revise identifications and to make some important corrections. A list of the preserved samples is given in the Appendix.

River Tees

Gammarus pulex L. Penetration into section I of the estuary, at Yarm, is confirmed, in shore and shrimp-trawl collections. Here it mixes with the more abundant *G. z. zaddachi* (see below). Casual specimens may well occur further down the estuary in the plankton in winter, but the statement 'occasional in plankton down to [section] VII' should be taken with reserve, as two out of five samples labelled '*G. pulex*' from other stations were, in fact, *G. zaddachi.*

G. zaddachi Sexton. This was entirely overlooked in the Tees. The typical subspecies, abundant in the upper half of the estuary, was wrongly attributed to *G. duebeni* (sometimes to *G. pulex*). All statements under the heading of '*duebeni*', as affecting the River Tees, should be transferred to *G. z. zaddachi.* Samples have been confirmed from the following sections: I, overlapping *G. pulex*, but more numerous; II and III, where evidently abundant, and the only species; IV, in the tidal zone under *Fucus*, where occurred a mixed population of this and *duebeni*; and in several tow-nettings. Another sample, labelled '*G. duebeni*', proved to be exclusively *G. z. zaddachi.* Unfortunately no samples survive from the main stream or low-water region of sections IV–VII, but it may be assumed that all the '*G. duebeni*' recorded from here are the typical subspecies of *zaddachi.* Had *G. zaddachi salinus* occurred in this region, it would presumably have been recorded as '*G. locusta*', as in the Tay. No evidence can be found for the existence of *salinus* anywhere in the Tees, and it is significant that the centre of its expected range coincides with the polluted zone between Stockton and Middlesbrough, where a wide—and quite abnormal—gap occurred in the *Gammarus* population.

G. duebeni Lillj. This species may be expected to occur sporadically in the tidal zone where fresh-water streams or seepage make permanent pools of more or less brackish consistency. It has been confirmed only from the tidal region in section IV, where a number were taken under *Fucus vesiculosus* in company with the preceding species.

G. locusta (L.). The range as given, sections XIII and XII intertidally, and in tow-nettings up to IX, is probably entirely correct, as these zones fall well within the anticipated range (up to IX or X in summer and X or XI in winter). One sample tube labelled '*G. locusta*' contains this species only. There are also several in a sample of mixed amphipods from section XIII; and others in tow-nettings labelled 'T21B', 'T23' and 'T25'.

Marinogammarus marinus (Leach). There is no opportunity of confirming the species of this genus, except for some true *marinus* from section XIII.

However, the reported distribution of *marinus* from XIII to X intertidally may be taken as correct. The bottom records for XIII to XI and in S XII are more likely to refer to *M. finmarchicus* Dahl (see below).

It will subsequently be shown that the revised picture of distribution of the different species conforms with results obtained from other British estuaries, though the Tees presents one outstanding peculiarity which clearly demands a special explanation. This is the complete break in the continuity of the *Gammarus* population between sections VII and X. In a normal river this gap would be bridged by a slight upward extension of *G. locusta* and by the dominant presence of *G. zaddachi salinus*, which appears to be completely absent. (The last, if present, should overlap *G. z. zaddachi* about up to section VI.) *M. marinus* should occur intertidally at least to section VII. The argument that the poverty of the fauna in this region of the Tees is due to pollution, if otherwise unproved, would have been very strongly reinforced by this further analysis of the *Gammarus* populations.

This point is worth further emphasis. It is now established that *Gammarus* populations remain dense throughout the length of an estuary, and numbers are not affected by the rigorous conditions of the mid-estuary region which reduces the variety of animal forms to a minimum. This is possible because a succession of forms (species or subspecies), each adapted to a special salinity range, and each overlapping its neighbours, occupies the whole stretch from the fresh-water river to the sea. The only natural limiting factor which may effectively reduce numbers is absence of suitable cover. But almost any available cover is made use of, varying from growing weeds to decomposing rubbish, and is never so lacking as to eliminate gammarids altogether. In the middle region of the Tees there is evidently, from accounts, sufficient cover to support a population of *Gammarus*, and absence of the latter indicates some effective polluting agency. Furthermore, since gammarids are not eliminated by contamination of waters with sewage or rubbish, it could be concluded that industrial effluents containing a significant concentration of some toxin was causing pollution. Poisoning was in fact found to be due to cyanides.

River Tay

G. pulex. Amongst material which Mrs Sexton has kindly shown me is a pair of *G. pulex* from the River Tay near Elcho, 21. i. 32. This locality is near the limit of tidal influence in the main river, but well away from the influence of brackish water. So far as we know the species is uncommon in the soft waters of Scottish rivers. It is not recorded in the Survey Report from the River Earn, which was chosen for following the conditions at the very upper limit of tidal influence.

G. zaddachi. This species was correctly recognized in some samples, but only the typical subspecies in the upper part of its range. *G. z. zaddachi* was correctly recorded from the bottom and tidal zones of sections I–IV. But it occurs equally in samples from various other sections down to X. Here again there was confusion with *G. duebeni*, but the latter species occurred intertidally with greater frequency than is usual (see below). In the upper part of its extensive range in the Tay, i.e. in sections I–IV, or Bridge of Earn to Newburgh, it was colonizing fresh water or water rarely greatly raised in salinity. This tendency is now known to be a usual feature. Characteristically too, the animals from these sections are of a small size and appear to show inhibited development: they were probably not reproducing.

In sections IX and X, in which *G. z. zaddachi* was becoming scarcer, examples of a 'saline' or 'non-hairy' form of *G. zaddachi* occur.† These had presumably been recorded as *G. locusta*, since none of the latter was found in samples higher than section XI, which represents indeed the predictable upper limit. The seaward limit of *G. zaddachi* in the Tay cannot be determined, through paucity of preserved specimens from XI, and their absence from XII and XIII.

G. duebeni Lillj. This species, as will be shown elsewhere, does not normally form a member of the estuarine succession, but occurs on the edge of the tidal zone and intertidally where special conditions exist—e.g. marked fresh-water seepage from the land. It appears, however, to have been genuinely more plentiful in the Tay estuary than is usual. Recorded as 'abundant between tidemarks from sections V–X', it has been confirmed in the following samples: V [tidal zone], a number of well-grown adults; VI, tidal zone, large sample in which *G. z. zaddachi* was mixed; VII, tidal zone, large sample in which *G. z. zaddachi* was nearly as plentiful; IX, high-water level, a number of adults (but none low-water level); X, mid-tide level, 39 well-grown adults. The record for the bottom in VI should be referred to *G. z. zaddachi* (four samples are entirely of this species).

G. locusta (L.). As pointed out above, the occurrence in sections IX and X should be referred to *G. zaddachi*. It genuinely occurs, however, in section XI, at least at near high-water level. Unfortunately the surviving samples from this zone are scanty, and there are none preserved from sections XII and XIII. The species, however, may be assumed to inhabit the seaward end of the estuary from XI onwards.

Marinogammarus marinus (Leach). The correct range was originally given, and the species appears to be normally plentiful in the upper part of the tidal zone, up the estuary to section VIII. It was also well distributed down to low water in sections IX–XI. In section XI, however, the next species was found mixed up with it.

M. finmarchicus (Dahl), a species unknown at the time of the survey, can be added to the fauna of the Tay Estuary, as already reported (Sexton & Spooner, 1940). It was, indeed, in revising the Tay material that the writer first recognized the occurrence of this distinct species in the British Isles, though it has proved easy to collect it below the Plymouth Laboratory. Normally marine intertidal, with the centre of its distribution in the lower half of the tidal zone, it does not appear to extend very far into estuaries, but a stony ground may be essential to it. In the Tay section XI appears to be its upper limit.

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† Not the true *G. z. salinus*, but a form with a more sparsely-haired and shorter antenna 1 peduncle: see p. 43.

The revised picture of distributions again agrees in essential respects with those from estuaries in the south of England. It is incomplete at the lower end, but it would appear that the zone in which a 'saline' form of *Gammarus zaddachi* forms 100% (or nearly so) of the *Gammarus* population is quite narrow. But it is important to remember that the summer and winter distributions are not distinguished. Special features are provided by the unusual abundance of *G. duebeni* in the tidal zone, by the penetration of *Marinogammarus finmarchicus* up to, or even beyond, the limit of *Gammarus locusta*, and by the apparent replacement of *G. z. salinus* by a form more closely akin to the northern *G.* '*locusta*' (see p. 43). The dominance of *G. z. zaddachi* for such a long stretch in the upper parts of the estuary is noteworthy, but quite in keeping with its habits elsewhere. It would be interesting to know how far it succeeds in reproducing above the level of Newburgh.

Certain difficulties encountered by Bassindale (1942*a*, p. 138 *et seq.*) in his attempt at comparing the zones occupied by different *Gammarus* spp. in several rivers, are now disposed of.[1] In the Tay *G. locusta* appeared to penetrate further up river than usual, but this was only because the 'saline' form of *G. zaddachi* had been overlooked, and even in section XI of the river *G. locusta* has only been confirmed from the high-water zone. *G. z. zaddachi* had also been overlooked from sections V to X, so that *G. duebeni* finds its proper place as a colonizer of the intertidal zone, and not as an interloper in the main *locusta-zaddachi-pulex* succession.

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[1] Bassindale was mistaken in supposing that all the Tay identifications were correct.

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APPENDIX

Tees Survey Collections: Samples Examined

River Tees

Section of river	Label on tube	Revised naming	Remarks
I	A. Yarm, 17. ix. 31, shore	*G. pulex*, 3 *G. z. zaddachi*, 9: 5 ♂♂, 2 ♀♀, 2 imm.	
I	A. Shrimp trawl, 8. x. 31	*G. pulex*, 1 very large ♂ *G. z. zaddachi*, 5 ♂♂, 3 ♀♀, 12 imm.	
II	B. White House and Barwick, shore, 17. ix. 31	*G. z. zaddachi*, large no. adults and imm.	
II	B. Shrimp trawl, 8. x. 31	*G. z. zaddachi*, 13: 5 ♂♂, 4 ♀♀, 4 imm.	
III	C. Above Preston Hall, shore, 17. ix. 31	*G. z. zaddachi*, 34: 26 ♂♂, 7 ♀♀, 1 imm.	
III	C. Shrimp trawl, 8. x. 31	*G. z. zaddachi*, several ♂♂, with 1 ♀ and 2 imm.	
IV	Among *Fucus vesiculosus*, '*Gammarus duebeni*'	*G. duebeni*, 19: 12 ♂♂, 7 ♀♀, robust specimens *G. z. zaddachi*, 5: 4 ♂♂, 1 ♀, large	Intertidal
IV	D. Shrimp trawl, 8. x. 31	*G. z. zaddachi*, 8: 2 ♂♂, 3 ♀♀, 3 imm.	
?	'*Gammarus pulex . . . duebeni*', from 8	*G. z. zaddachi*, several large ♂♂	
?	'*Gammarus duebeni*'	*G. z. zaddachi*, 9: 6 ♂♂, 2 ♀♀, 1 imm.	
?	Tow-netting, 9	*G. z. zaddachi*, ♂	
?	Tow-netting, 7	*G. z. zaddachi*, large ♀ with eggs	
?	Tow-netting, 7B	*G. z. zaddachi*, 6: 5 ♂♂, 1 ♀, breeding	
?	Tow-netting, Q11	*G. z. zaddachi*, very large ♂	
?	Tow-netting, T21*b*	*G. locusta*, young ♂	
?	Tow-netting, T23	*G. locusta*, 2 young ♂♂, 5 ♀♀, several imm.	
?	Tow-netting, T25	*G. locusta*, 6: 2 ♂♂, 3 ♀♀, 1 imm.	
(XI–XIII)	'*Gammarus locusta*'	*G. locusta*, several	
XIII	'*Gammarus marinus* Leach'	*Gammarus locusta*, 13 *Marinogammarus marinus*, 7 *Amphithoë rubricata*, 1 *Melita palmata*, 2	
?	13. xii, 12. v. 30 '*Gammarus pulex*'	*G. pulex*, several	
?	O.I. 26. vi. 29 '*Gammarus pulex*'	*G. pulex*, two	
?	B9. 10. ii. 30 '*Gammarus pulex*'	*G. pulex*, 8	
?	A6. 18. xi. 29 '*Gammarus pulex*'	*G. z. zaddachi*, 3	
?	A56. 23. x. 29 '*Gammarus pulex*'	*G. z. zaddachi*, 3 ♂, 1 ♀	

River Tay

Section of river	Label on tube	Revised naming	Remarks. Recorded as:
I	Sect. I	*G. z. zaddachi*: adults and imm., dwarf	'*G. zaddachi*'
II	Sect. II	*G. z. zaddachi*, 49: 37 ♂♂, 4 ♀♀, 8 imm., dwarf	”
III	Sect. III	*G. z. zaddachi*: adults and imm., dwarf	”
IV	Sect. IV	*G. z. zaddachi*, several, dwarf	”
V (tidal zone)	Sect. V	*G. duebeni*, a number of well-grown adults	'*G. duebeni*'
VI	Sect. VI, tidal zone	*G. duebeni*, large sample, mainly well-grown adults	”
		G. z. zaddachi, 6: 5 ♂♂, 1 imm. (one ♂ dwarf)	”
”	Sect. VI, 13. Bottom	*G. z. zaddachi*, 7 imm.	”
”	Sect. VI, 14. Bottom	*G. z. zaddachi*, 11: 2 ♂♂, 2 ♀♀, 7 imm., dwarf	”
”	Sect. VI, 15. Bottom	*G. z. zaddachi*, several, maturing and imm., dwarf	”
”	Sect. VI. Bottom	*G. z. zaddachi*, dwarf, ♀ and 4 imm.	”
VIII	Sect. VIII. Tidal zone	*G. duebeni*, 67: 32 ♂♂, 32 ♀♀, 3 imm.; large	”
		G. z. zaddachi, 42: 19 ♂♂, 13 ♀♀, 10 imm., very variable in size, some large, some dwarf	”
		Marinogammarus marinus, 3: 2 ♂♂, 1 ♀	'*G. marinus*'
IX	Sect. IX. High-tide level	*G. duebeni*, a number of adults *M. marinus*, 1	'*G. duebeni*' '*G. marinus*'
IX	Sect. IX. Low-tide level	*M. marinus*, a number *G. z. zaddachi*, 1 ♂ *G. zaddachi*, 'saline' form, 5 ♂♂	'*G. marinus*' '*G. duebeni*' '*G. locusta*'
X	Sect. X. Mid-tide level	*G. duebeni*, 39: 20 ♂♂, 19 ♀♀, well grown	'*G. duebeni*'
X	Sect. X. Low-tide level	*G. z. zaddachi*, 6: 4 ♂♂, 1 ♀, 1 imm. *G. zaddachi*, 'saline' form, 5: 4 ♂♂, 1 ♀ *Marinogammarus marinus*, a number	'*G. duebeni*' '*G. locusta*' '*G. marinus*'
XI	Sect. XI. High-tide level	*Gammarus locusta*, 1 ♂ *Marinogammarus marinus*, 3 *M. finmarchicus*, 1 ♀	'*G. locusta*' '*G. marinus*' ”
XI	Sect. XI. Mid-tide level	*M. marinus*, numerous *M. finmarchicus*, 1 ♂	'*G. marinus*' ”
XI	Sect. XI. Low-tide level	*M. marinus*, many *M. finmarchicus*, 2 ♂♂, 2 ♀♀	'*G. marinus*' ”

OBSERVATIONS ON FLOUNDERS *PLEURONECTES FLESUS* L. MARKED IN THE ESTUARIES OF THE TAMAR AND LYNHER

By P. H. T. Hartley

From the Plymouth Laboratory

Introduction

In the winter of 1937–8 just over a thousand flounders (*Pleuronectes flesus* L.) were caught, marked and released in the estuaries of the rivers Tamar and Lynher which flow into the west end of Plymouth Sound. The objects of this marking experiment were three. First, to discover the distribution and migrations of the adult flounders which had spent the years of immaturity in the estuaries. Secondly, to obtain observational, as distinct from inductional, data upon the growth of the species. Thirdly, to study changes in the distribution of the stock of immature fish within the estuaries.

The first object of the investigation was not fulfilled. There was but a very small number of returns from the open sea: this may be in part due to the great limitation of fishing along the south coasts of England which resulted from the outbreak of war some 18 months after the marking was completed. The two returns from localities at a distance from Plymouth do no more than hint at possibilities. The information obtained on growth gave proof that the individual variation in growth rates observed by Cunningham (1896) in captive fish was also to be found in the wild, and showed that there is relatively little growth in the winter months. The 152 recoveries of flounders within the estuaries have shown the existence of seasonal movements and redistributions of the fish of the immature stock. It is highly improbable that any more marked fish will be returned, and the results obtained are now summarized.

The Marking Experiment

The flounders were caught with a 'Saltash Tuck-net' (see Hartley, 1940). On the grounds around Saltash, 659 fish were marked in thirteen netting expeditions between 23 September and 26 November 1937, most of the work being done at night. At Sheviock Wood, on the Lynher, 327 fish were marked in three days' work on 21 and 24 September and 20 October 1937. On the night of 7–8 October 1937, 12 flounders were marked on the West Mud ground. In addition, on 24 February 1938, 41 flounders were marked at Saltash with disks taken from fish already returned. A map of the area will be found in Hartley & Spooner (1938). Two places mentioned in this paper are not shown on the map. They are Cotehele, 2 miles up the Tamar above Halton Quay, and Calstock, which lies a mile upstream from Cotehele. Sandacre, also not marked on the map, is a spit of shoal ground in the Lynher below Forder Creek.

The flounders were kept in shallow baths of salt water until the strength of the tide put an end to fishing. Then each fish in turn was measured from the tip of the closed jaws to the end of the longest caudal ray, marked and at once released. There were no transplantation experiments. All the fish were released on the grounds where they had been caught and within an hour or two of the time of capture. The measurement was accurate to within ± 0·5 cm., this being the margin of error resulting from the measuring of a lively fish by the light of a hurricane lamp in an open boat on a winter's night. The marks were circular vulcanite disks of two sizes, 15 and 7·5 mm. in diameter. Two disks of the same diameter were used to mark each fish, a black disk to lie against the white under surface and a white disk, stamped with the initials PH and a serial number, to lie on the upper side. The white disk was placed with the numbered surface outwards. The disks were linked with a silver wire thrust through the dorsal musculature in the middle of the fish's length and about 1 cm. below the base of the dorsal fin. A little 'play' was allowed between the disks and the fish's flank, and in no case was any suppuration or necrosis of tissue found around the mark of a recovered specimen.

Printed posters were circulated to the waterside villages and to fishing ports, offering rewards for the return of marked fish.

148 flounders were returned between the beginning of marking and 5 May 1940, 116 of those marked at Saltash, 31 of the Sheviock fish and one from West Mud. Several marked flounders caught by Saltash fishermen were brought alive to the slip at that town. These fish were measured by Mr J. Gould and released a second time: seven were recovered again at a later date, and one was caught three times. Details of all recoveries are given in tabular form in the Appendix.

I am happy to be able to express my gratitude to Mr J. Gould for his help with the work of marking and the recording of recovered fish.

Recoveries at Sea

Of the four flounders recaptured in the sea two male fish, nos. PH 179 and 314 were found in 20–30 fathoms of water on the Looe-Eddystone ground, a known spawning area of the species a few miles south-west of Plymouth. A female fish, no. PH 497, was caught off Sharkham Point, south Devon, some 40 miles by sea to the east of Plymouth, and an unsexed fish, no. PH 815, was recovered 2 miles south of Brighton. This latter fish had made a journey of about 200 miles to the eastward.

Ehrenbaum (1908) found that flounders marked in the Elbe moved westward or south-westward along the coasts of the Low Countries, and had but one recovery from water more than 40 m. in depth. Redecke (1907) recorded the recovery of flounders, marked in the Zuider Zee, on the coasts of Belgium and France as far west as the mouth of the Seine. The two west-country flounders which had moved to a distance from Plymouth (if it be at all permissible to speculate on the import of evidence so small) had travelled in an opposite direction—to the eastward. Yet the emigrations of the flounders from the three areas had this in common, that they were all in the direction of relatively shallow water. Cunningham (1896) has remarked that this species is rarely found in more than 30 fathoms of water, and in the Baltic, Ehrenbaum (1911) observed that spent flounders moved away from the Bornholm Deeps to the shallows of the Pomeranian coast.

GROWTH

Some 80% of the flounders recovered were caught in the first 6 months after they had been marked, that is in the 'winter' period of October to March. Only a few of these fish had made good any appreciable growth in this period (Table I) within which the fast of the immature members of the stock also occurs (Hartley, 1940).

TABLE I. *PLEURONECTES FLESUS*, THE FLOUNDER. GROWTH OF MARKED FLOUNDERS SHOWING APPRECIABLE INCREMENT IN LENGTH DURING THE SIX WINTER MONTHS (OCTOBER TO MARCH) IMMEDIATELY AFTER MARKING

When a fraction of a month is to be considered, 16 days or more are counted as a complete month, 15 days or less are not counted.

No. PH	Date of marking	Length at marking (cm.)	Date of recovery	Length at recovery (cm.)	Increment in length (cm.)	Months since marking	Mean increment in length per month (cm.)
			Females				
9	21. ix. 37	24·2	30. xii. 37	25·8	1·6	3	0·53
328	3. xi. 37	27·0	3. ii. 38	28·0	1·0	3	0·33
			Males				
115	6. x. 37	22·5	1. ii. 38	25·2	2·7	4	0·675
193	13. x. 37	19·6	7. ii. 38	20·6	1·0	4	0·25
337	12. xi. 37	20·5	12. ii. 38	21·5	1·0	3	0·33
371	12. xi. 37	21·6	19. ii. 38	23·3	1·7	3	0·57
893	12. xi. 37	19·6	9. ii. 38	21·2	1·6	3	0·53

In Table II are shown the increases in length of all marked flounders which had been at liberty for more than 6 months, with the average increment per month of liberty and also the average increment per month of liberty between the months of April to September inclusive. These are the months of regular feeding and higher 'condition' (Hartley, 1940), and it may be inferred both

TABLE II. *PLEURONECTES FLESUS* THE FLOUNDER. GROWTH OF ALL MARKED FLOUNDERS WHICH HAD BEEN AT LIBERTY FOR MORE THAN SIX MONTHS, WITH INCREMENT IN LENGTH PER MONTH OF LIBERTY, AND ALSO INCREMENT FOR EACH 'SUMMER' MONTH (APRIL TO SEPTEMBER) AFTER MARKING

When a fraction of a month is to be considered, 16 days or more are counted as a complete month, 15 days or less are not counted.

No. PH	Date of marking	Length at marking (cm.)	Date of recovery	Length at recovery (cm.)	Increment in length (cm.)	Months since marking	Mean increment in length per month since marking (cm.)	'Summer' months since marking	Mean increment in length per 'summer' month since marking (cm.)
				Females					
4	21. ix. 37	35·4	11. ix. 38	36·2	0·8	12	0·067	6	0·13
61	24. ix. 37	36·4	7. viii. 38	36·5	0·1	10	0·01	4	0·025
65	24. ix. 37	36·6	26. vi. 38	36·6	0	9	0	3	0
76	24. ix. 37	27·4	12. ix. 38	31·2	3·8	12	0·32	6	0·63
112	24. ix. 37	18·6	10. vi. 38	21·2	2·6	9	0·29	3	0·87
236	13. x. 37	19·1	8. viii. 38	25·4	6·3	10	0·63	4	1·57
272	15. x. 37	20·3	3. vi. 38	21·0	0·7	8	0·09	2	0·35
276	15. x. 37	20·1	17. v. 38	20·6	0·5	7	0·07	2	0·25
296	20. x. 37	36·6	15. x. 39	39·75	3·15	24	0·13	12	0·26
298	20. x. 37	37·5	12. ix. 38	38·6	1·1	11	0·1	5	0·22
321	22. x. 37	26·2	17. v. 38	29·0	2·8	7	0·4	2	1·4
363	12. xi. 37	21·2	2. x. 38	30·6	9·4	11	0·85	6	1·57
380	12. xi. 37	19·8	29. vi. 38	23·2	3·4	8	0·425	3	1·13
391	25. xi. 37	20·0	5. v. 40	37·7	17·7	29	0·61	13	1·36
				Males					
57	24. ix. 37	26·6	14. viii. 38	29·4	2·8	11	0·25	5	0·56
268	15. x. 37	19·1	11. ix. 38	22·0	2·9	11	0·26	5	0·58
280	15. x. 37	20·9	3. vi. 38	22·4	1·5	8	0·19	2	0·75
445	25. xi. 37	23·0	2. v. 40	30·3	7·3	29	0·25	13	0·56
479	25. xi. 37	20·0	29. vi. 38	23·2	3·2	7	0·46	3	1·07
496	26. xi. 37	33·0	26. viii. 38	33·0	0	9	0	5	0
525	21. ix. 37	16·3	11. ix. 38	24·6	8·3	12	0·69	6	1·38
535	21. ix. 37	16·4	25. v. 38	16·9	0·5	8	0·06	2	0·25
619	6. x. 37	16·8	29. vi. 38	19·0	2·2	9	0·24	3	0·73
788	20. x. 37	11·8	14. viii. 38	18·2	6·4	10	0·64	4	1·6
888	12. xi. 37	17·7	11. ix. 38	25·0	7·3	10	0·73	5	1·46

from this fact and from the observed lack of growth in fish recaptured in their first winter that these are also the months when most, if not all, of the increase in size is made.

There is obviously great individual variation in both sexes, and it is not possible to make generalizations from these data, though it may be pointed out that the swiftest growth rates are shown by some of the smallest fish. Two flounders marked in Poole Harbour made growths of 8·5 cm. from a length at marking of 21·5 cm., and of 5·5 cm. from a length at marking of 24·5 cm., between 9 October 1925 and the end of May 1927 (Buchanan-Wollaston, 1933). The mean length increments per month of the two fish, 0·425 and 0·275 cm., and the mean increments per 'summer' month of 1·06 and 0·69 cm. are of the same order as those found in flounders from the estuaries of the Tamar and Lynher.

There is individual variation not only in the growth rates but also in the maximum lengths attained. Among the female fish, nos. PH 61 and 65 had reached their full growth of 36·4 and 36·6 cm. at the time of marking. Nos. PH 4 and 298 grew by 0·8 and 1·1 cm. in a year from lengths at marking of 35·4 and 37·5 cm., and no. PH 296 grew by 3·15 cm. in 2 years, although she was already 36·6 cm. in length when she was marked. Only one fully grown male fish was recovered, no. PH 496 which made no growth in 9 months from a length at marking of 33·0 cm.

Movements within the Estuaries

Flounders marked on the Saltash Grounds

Of the fish marked in the autumn on the Saltash grounds the greater number remained in the immediate vicinity through the winter. Those which did move away went short distances downstream to the shores of the Hamoaze. From the end of March onwards recoveries from the upper reaches of the estuaries, especially around Cotehele, began to come in suggesting a movement of part of the population upstream. It is generally believed by the local fishermen that there is such a spring movement away from the sea of those fish which will summer in the rivers, and the recaptures in the first summer after marking give concrete evidence of its existence. A female flounder, no. PH 240, for example, was marked at Saltash on 15 October 1937, recovered at the same place on 12 December and again released, to be taken a third time at Cotehele Quay on 7 April 1938; another female flounder, no. PH 272, also marked at Saltash on 15 October was recaptured and liberated again at the place of marking on 3 February 1938, and caught once more on 3 June 1938, at Cotehele Quay. It must, however, be pointed out that there is a great increase in the amount of netting in the upper reaches of the estuaries after the opening of the salmon season on 1 March and it is not certain that all the fish taken after that date well above the place of marking had but recently moved away from the seaward grounds. Recoveries such as those of nos. PH 240 and 272 suggest that the redistribution of the stock does not take place until the spring, but do not prove it. The arithmetic mean length at the time of marking of the flounders which had moved downstream from the place of marking was 22·5 cm., and the arithmetic mean length of the fish which had gone upstream was 19·93 cm. The difference between these mean lengths is statistically significant, and confirms the existence of a reassortment of the stock before the breeding season, the larger fish going downstream to the sea, the smaller fish up the river to the more brackish stretches.

Only two flounders were recovered in the Tavy, a male fish no. PH 619 taken at Maristow on 29 June 1938, and a spent female no. PH 391 from Bere Ferrers in May 1940. The latter fish must have been down to the sea at least once to spawn. The two male flounders, nos. PH 268 and 888, marked at Saltash and recovered at Sheviock Wood may have been down to the sea to spawn, for both were large enough to have been mature fish.

Flounders marked at Sheviock Wood

Of the fish marked at Sheviock Wood a number moved downstream to the Hamoaze or to the last reaches of the Tamar at Saltash. Three of the fish which went downstream, a female no. PH 112 and two males, nos. PH 38 and 535, were recovered well up the Tamar in the spring and early summer after marking. All three were under 19 cm. long at the time of marking, and it is probable that they had taken part in the spring-time movement upstream from the Saltash marks. One fish, no. PH 14, was recaptured at St Germans, 1½ miles upstream about 3 weeks after it was marked on 21 September 1937.

There is relatively little netting at Sheviock Wood and it was scarcely to be expected that there would be as many recoveries at the place of marking as were made at Saltash. A male fish, no. PH 59, was marked at Sheviock on 24 September 1937, and recaptured there on 20 October of the same year: by 11 January 1938, it had moved downstream to Petre's, in the Hamoaze. Two other male fish, no. PH 525 marked on 21 September 1937, and no. PH 788, marked on 20 October 1937, were recovered at Sheviock on 11 September 1938, and 14 August 1938 respectively. An unsexed flounder, no. PH 765, was marked at Sheviock on 20 October 1937, and recaptured there on 14 August 1938. The other flounders marked at Sheviock Wood and recovered on the same ground, or farther upstream, had probably been down to the sea and returned again.

SUMMARY

1039 flounders were marked with numbered vulcanite disks in the estuaries of the Tamar and Lynher.

148 flounders were recaptured and of these seven fish were recovered a second time after one recovery and release, and one fish was recaptured on three occasions after two previous recoveries and releases.

Only two fish were recovered at a distance from Plymouth. Both had moved eastward, up the English Channel.

There was little or no growth in the winter months.

Individual growth rates were found to vary greatly.

The flounders living in the last reach of the Tamar near Saltash tended to remain in one limited area during the winter months, save for a drift downstream of some of the larger fish. In the spring there was an upstream movement of the smaller, immature fish.

Flounders which had gone down to the sea to spawn might return to the river in which they were marked, or to the other river of the two which join to form the Hamoaze, or they might move right away from the area where they were marked.

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APPENDIX

Recoveries of flounders marked in the estuaries of the rivers Tamar and Lynher 1937 and 1938

		At marking		Recoveries				Length at recovery (cm.)
No. PH	Sex	Date (1937)	Length (cm.)	Where marked	Upstream of marking place	Downstream of marking place	Other localities	
Marked at Saltash, river Tamar								
53	♀	23. ix.	22·5	15. x. 37	—	—	—	—
(Second recovery)				6. xii. 37	—	—	—	22·5
54	—	23. ix.	21·9	—	—	Keyham Creek 28. xi. 37	—	—
115	♂	6. x.	22·5	—	—	Keyham Creek 1. ii. 38	—	25·2
122	—	6. x.	18·7	15. x. 37	—	—	—	—
124	—	6. x.	20·8	13. xi. 37	—	—	—	20·8
126	♀	6. x.	18·1	—	—	Eastern Ground 7. x. 37	—	—
(Second recovery after release at Saltash)				*c.* 30. xii. 37	—	—	—	18·5
130	—	6. x.	19·3	—	—	Rats Island 14. x. 37	—	—
(Second recovery after release at Saltash)				14. x. 37	—	—	—	—
133	♀	6. x.	21·2	24. x. 37	—	—	—	21·4
136	♀	6. x.	19·6	7. ii. 38	—	—	—	—
(Second recovery)				9. ii. 38	—	—	—	—
(Third recovery)				26. ii. 38	—	—	—	19·8
137	♂	6. x.	21·8	—	—	West Mud *c.* 1. ii. 38	—	22·7
153	—	6. x.	19·4	15. x. 37	—	—	—	—
173	—	13. x.	26·6	18. xi. 37	—	—	—	—
179	♂	13. x.	24·9	—	—	—	Looe-Eddystone Ground 1. iii. 38	25·6
183	—	13. x.	22·4	—	—	Weston Mill Lake 23. xi. 37	—	—
188	♀	13. x.	22·7	25. xi. 37	—	—	—	—
(Second recovery)				24. i. 38	—	—	—	22·5
189	♀	13. x.	18·8	30. x. 37	—	—	—	18·8
193	♂	13. x.	19·6	7. ii. 38	—	—	—	20·6
196	—	13. x.	23·1	1. ii. 38	—	—	—	23·8
213	—	13. x.	22·2	9. i. 38	—	—	—	22·8
216	♀	13. x.	20·1	12. xi. 37	—	—	—	20·1
221	♀	13. x.	20·3	13. i. 38	—	—	—	19·5
229	—	13. x.	18·4	8. ii. 38	—	—	—	18·6
232	♂	13. x.	19·0	7. ii. 38	—	—	—	18·9
234	—	13. x.	18·8	3. ii. 38	—	—	—	18·5
236	♀	13. x.	19·1	—	R. Tavy 8. viii. 38	—	—	25·4
240	♀	15. x.	25·8	12. xii. 37	—	—	—	25·8
(Second recovery)				—	Cotehele Quay 7. iv. 38	—	—	25·5

No. PH	Sex	At marking		Recoveries				Length at recovery (cm.)
		Date (1937)	Length (cm.)	Where marked	Upstream of marking place	Downstream of marking place	Other localities	
250	—	15. x.	26·7	9. ii. 38	—	—	—	27·7
264	♀	15. x.	21·6	2. xi. 37	—	—	—	21·5
267	—	15. x.	23·9	10. i. 38	—	—	—	24·0
268	♂	15. x.	19·1	—	—	—	Sheviock Wd. R. Lynher 11. ix. 38	22·0
270	—	15. x.	24·4	9. ii. 38	—	—	—	25·4
272	♀	15. x.	20·3	3. ii. 38	—	—	—	20·7
(Second recovery)				—	Cotehele Quay 3. vi. 38	—	—	21·0
276	♀	15. x.	20·1	—	Cotehele Quay 17. v. 38	—	—	20·6
277	♀	15. x.	19·5	12. xi. 37	—	—	—	—
280	♂	15. x.	20·9	—	Cotehele Quay 3. vi. 38	—	—	22·4
283	—	15. x.	21·8	28. x. 37	—	—	—	22·0
287	♂	15. x.	21·7	—	Cotehele Quay 12. iii. 38	—	—	22·1
319	—	21. x.	26·2	21. i. 38	—	—	—	26·6
321	♀	22. x.	26·2	—	Cotehele Quay 17. v. 38	—	—	29·0
328	♀	3. xi.	27·0	—	—	Petre's 3. ii. 38	—	28·0
334	♀	12. xi.	19·8	10. ii. 38	—	—	—	20·0
337	♂	12. xi.	20·5	—	—	Weston Mill Lake 12. ii. 38	—	21·5
343	—	12. xi.	21·7	23. ii. 38	—	—	—	23·5
362	♀	12. xi.	24·8	5. ii. 38	—	—	—	25·4
363	♀	12. xi.	21·2	—	—	Cove Rock 2. x. 38	—	30·6
370	♀	12. xi.	21·4	—	—	Bull Point 21. xi. 37	—	21·4
71	♂	12. xi.	21·6	9. ii. 38	—	—	—	23·3
7	—	12. xi.	22·2	9. i. 38	—	—	—	22·4
80	♀	12. xi.	19·8	—	Cotehele Quay 29. vi. 38	—	—	23·2
391	♀	25. xi.	20·0	—	Bere Ferrers, R. Tavy 5. v. 40	—	—	37·7
409	♂	25. xi.	30·2	—	—	Henn Point 21. v. 38	—	29·7
434	♂	25. xi.	23·2	—	—	Lower Petre's 4. i. 38	—	23·5
435	—	25. xi.	24·2	12. xii. 37	—	—	—	24·3
437	♂	25. xi.	27·3	25. xii. 37	—	—	—	27·9
440	♂	25. xi.	23·1	—	—	Petre's 13. i. 38	—	23·5
442	—	25. xi.	22·3	12. xii. 37	—	—	—	22·3
445	♂	25. xi.	23·0	—	Hole's Hole 2. v. 40	—	—	30·3
448	♀	25. xi.	25·5	12. xii. 37	—	—	—	25·4
455	♀	25. xi.	22·5	30. xii. 37	—	—	—	22·5

No. PH	Sex	At marking		Recoveries				Length at recovery (cm.)
		Date (1937)	Length (cm.)	Where marked	Upstream of marking place	Downstream of marking place	Other localities	
460	—	25. xi.	21·8	23. i. 38	—	—	—	22·6
472	♂	25. xi.	23·5	30. xii. 37	—	—	—	23·4
475	—	25. xi.	22·6	30. i. 38	—	—	—	22·8
479	♂	25. xi.	20·0	—	Neill Quay 29. vi. 38	—	—	23·2
483	♂	26. xi.	22·4	16. xii. 37	—	—	—	22·4
488	♀	26. xi.	23·6	30. xii. 37	—	—	—	23·3
496	♂	26. xi.	33·0	—	Neill Point 26. viii. 38	—	—	33·0
497	♀	26. xi.	27·8	—	—	—	Sharkham Pt, S. Devon 24. iii. 38	27·8
568	♀	23. ix.	12·9	30. i. 38	—	—	—	13·0
616	—	6. x.	18·8	3. ii. 38	—	—	—	19·1
619	♂	6. x.	16·8	—	Maristow, R. Tavy 29. vi. 38	—	—	19·0
621	—	6. x.	16·6	15. x. 37	—	—	—	—
626	♂	13. x.	19·5	28. x. 37	—	—	—	19·8
628	♀	13. x.	16·7	—	2 miles below Calstock 23. iii. 38	—	—	17·3
630	—	13. x.	19·1	*c.* 2. x. 38	—	—	—	25·3
636	♂	13. x.	18·6	26. i. 38	—	—	—	18·6
645	♀	13. x.	18·5	5. ii. 38	—	—	—	18·9
650	♂	15. x.	13·1	—	Cotehele 29. iii. 38	—	—	13·6
652	♂	15. x.	11·3	26. ii. 38	—	—	—	11·9
656	—	15. x.	—	13. xi. 37	—	—	—	—
668	♀	15. x.	19·5	26. ii. 38	—	—	—	19·7
677	♀	15. x.	19·5	28. x. 37	—	—	—	19·6
682	♂	15. x.	19·1	12. xii. 37	—	—	—	18·9
685	♀	15. x.	19·3	—	—	Eastern Gd. 27. i. 38	—	19·4
698	—	15. x.	19·2	21. i. 38	—	—	—	20·1
700	—	15. x.	20·0	28. xi. 37	—	—	—	20·1
706	♀	15. x.	19·2	28. x. 37	—	—	—	—
707	♀	15. x.	21·0	11. xii. 37	—	—	—	20·8
711	♀	15. x.	20·3	—	—	West Mud 17. i. 38	—	20·9
800	—	21. x.	21·0	28. x. 37	—	—	—	21·1
815	—	22. x.	19·4	—	—	—	2 miles south of Brighton 10. iii. 39	28·0
821	—	22. x.	19·0	1. ii. 38	—	—	—	19·2
830	—	22. x.	17·0	2. ii. 38	—	—	—	17·4
845	♀	22. x.	12·0	25. xii. 37	—	—	—	12·5
869	♀	3. xi.	19·2	24. xi. 37	—	—	—	—
888	♂	12. xi.	17·7	—	—	—	Sheviock Wd, R. Lynher 11. ix. 38	25·0
893	♂	12. xi.	19·6	9. ii. 38	—	—	—	21·2
897	♂	12. xi.	17·9	4. ii. 38	—	—	—	18·5
911	—	12. xi.	18·5	9. i. 38	—	—	—	18·6
912	♂	12. xi.	17·2	30. i. 38	—	—	—	17·5
919	♂	12. xi.	18·6	7. ii. 38	—	—	—	18·7
920	—	12. xi.	17·0	10. ii. 38	—	—	—	17·2
929	♀	25. xi.	19·2	26. xi. 37	—	—	—	19·2
931	♂	25. xi.	19·3	28. i. 38	—	—	—	19·2

No. PH	Sex	At marking: Date (1937)	At marking: Length (cm.)	Recoveries: Where marked	Recoveries: Upstream of marking place	Recoveries: Downstream of marking place	Recoveries: Other localities	Length at recovery (cm.)
947	♀	25. xi.	21·0	18. xii. 37	—	—	—	20·8
948	—	25. xi.	19·4	26. i. 38	—	—	—	19·2
949	♀	25. xi.	20·6	27. ii. 38	—	—	—	20·5
962	—	25. xi.	17·3	9. ii. 38	—	—	—	17·1
963	♀	25. xi.	21·0	12. xii. 37	—	—	—	21·4
980	♂	26. xi.	19·7	11. xii. 37	—	—	—	19·6
983	—	26. xi.	18·7	8. i. 38	—	—	—	19·0
987	—	26. xi.	18·0	7. ii. 38	—	—	—	18·2
216/2	♀	26. xi.	22·5	25. xii. 37	—	—	—	22·3
59/2	♀	(1938) 24. ii.	21·5	—	Cotehele Quay 23. v. 38	—	—	22·1
370/2	—	24. ii.	18·5	—	Cotehele 14. iii. 38	—	—	—
448/2	♀	24. ii.	17·5	—	2 miles below Calstock 23. iii. 38	—	—	17·2
592/2	♀	24. ii.	13·7	27. ii. 38	—	—	—	13·6

Marked at West Mud

160	—	(1937) 7. x.	17·2	Recovered at Saltash, 27. x. 37.

Marked at Sheviock Wood, River Lynher

4	♀	21. ix.	35·4	11. ix. 38	—	—	—	36·2
5	—	21. ix.	22·6	24. ix. 37	—	—	—	22·6
9	♀	21. ix.	24·2	—	—	Weston Mill Lake 30. xii. 37	—	25·8
14	—	21. ix.	23·6	—	St German's Quay 15. x. 37	—	—	—
20	—	21. ix.	19·4	24. ix. 37	—	—	—	—
38	♂	21. ix.	18·9	—	—	—	Hole's Hole, R. Tamar 20. iv. 38	17·8
57	♂	24. ix.	26·6	14. viii. 38	—	—	—	29·4
59	♂	24. ix.	23·5	20. x. 37	—	—	—	—
(Second recovery)				—	—	Petre's 11. ii. 38	—	23·9
61	♀	24. ix.	36·4	7. viii. 38	—	—	—	36·5
65	♀	24. ix.	36·6	—	—	Henn Point 26. vi. 38	—	36·5
74	—	24. ix.	24·3	—	—	Saltash 9. i. 38	—	25·0
76	♀	24. ix.	27·4	—	St German's Quay 12. ix. 38	—	—	31·2
86	♂	24. ix.	25·1	—	—	Saltash 8. xi. 37	—	25·0
102	♂	24. ix.	23·2	—	—	Cove Rock 11. i. 38	—	23·7
112	♀	24. ix.	18·6	—	—	—	Halton Quay, R. Tamar 10. vi. 38	21·2

		At marking		Recoveries				
No. PH	Sex	Date (1937)	Length (cm.)	Where marked	Upstream of marking place	Downstream of marking place	Other localities	Length at recovery (cm.)
288	—	20. x.	35·1	—	—	Eastern Ground 30. xii. 37	—	35·2
293	—	20. x.	35·2	—	—	Saltash 3. vi. 38	—	—
296	♀	20. x.	36·6	—	—	Saltash 15. x. 39	—	39·75
298	♀	20. x.	37·5	—	St German's Quay 12. ix. 38	—	—	38·6
310	♂	20. x.	24·4	—	—	Henn Point 4. ii. 38	—	24·6
314	♂	20. x.	27·3	—	—	—	Looe-Eddystone Ground 15. ii. 38	30·2
317	—	20. x.	23·6	—	—	Rat's Island 25. xi. 37	—	—
513	—	21. ix.	16·6	24. ix. 37	—	—	—	—
525	♂	21. ix.	16·3	11. ix. 38	—	—	—	24·6
535	♂	21. ix.	16·4	—	—	—	Cotehele Quay, R. Tamar 25. v. 38	16·9
558	♀	21. ix.	15·8	—	—	Sandacre 1. x. 37	—	—
592	♂	24. ix.	15·1	—	—	Keyham Creek 13. i. 38	—	15·1
758	—	20. x.	17·6	—	—	Cove Rock 24. i. 38	—	17·5
765	—	20. x.	17·9	17. xii. 37	—	—	—	—
775	♀	20. x.	19·1	—	—	West Mud 4. i. 38	—	19·3
788	♂	20. x.	11·8	14. viii. 38	—	—	—	18·2

A number of the flounders marked by Ehrenbaum (1908) showed an apparent *decrease* in length between the times of marking and recovery similar to that shown by several of the fish from the Tamar and Lynher.

THE SPAWNING OF MACKEREL, *SCOMBER SCOMBRUS* L., AND PILCHARD, *CLUPEA PILCHARDUS* WALBAUM, IN THE CELTIC SEA IN 1937–39

WITH OBSERVATIONS ON THE ZOOPLANKTON INDICATOR SPECIES, *SAGITTA* AND *MUGGIAEA*

By P. G. Corbin, B.A.
Zoologist at the Plymouth Laboratory

(Text-figs. 1–21)

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Introduction

Large shoals of mackerel collect each spring in the waters to the south of Ireland and off the western entrance to the English Channel. In 1936, at the instance of the Ministry of Agriculture and Fisheries, the Marine Biological Association of the United Kingdom started an investigation of the biology of this mackerel population of the Celtic Sea.

One of the aims of the investigation was to determine the duration and locality of spawning of the mackerel and the distribution of the pelagic young stages. To this end, a survey of the plankton and hydrology of the area was carried out during a series of cruises in the years 1937, 1938 and 1939. Joint co-operation in the programme of cruises by the Fisheries Departments of

Eire and France was agreed at a meeting of the Mackerel Sub-Committee of the International Council for the Exploration of the Sea held at the Plymouth Laboratory in December 1937 (Le Danois, 1939*a*, *b*). The following cruises were made:

1937

12–20 April	S.S. *George Bligh* (United Kingdom)
27–30 May	Steam drifter *B.T.B.*, L.T. 1153 (U.K.)
20–22 July	Steam trawler *Elk*, M. 36 (U.K.)

1938

23 March–5 April	S.S. *Quentin Roosevelt* (France)
6–9 April	S.S. *Quentin Roosevelt* (France)
7–12 April	S.S. *Muirchu* (Eire)
7–18 April	S.S. *George Bligh* (U.K.)
31 May–5 June	S.T. *Elk* (U.K.)
19–24 July	S.T. *Elk* (U.K.)

1939

15–18 March	S.T. *Elk* (U.K.)
16–27 April	S.S. *George Bligh* (U.K.)
17–21 April	S.S. *Muirchu* (Eire)
2–7 June	S.T. *Elk* (U.K.)

Some of the results of this programme of research have already been published. Farran (1939) has described the distribution of mackerel eggs and young stages taken in April 1938 to the south of Ireland by the Irish Fishery Cruiser *Muirchu*. Extensive data resulting from the two cruises made in March and April 1938 by the French Research Ship *Quentin Roosevelt* have been fully reported by Furnestin (1939*a*), and an introductory account of the distribution of mackerel eggs and young stages in the area covered by the Plymouth cruises is included in preliminary reports of the work of the investigation at Plymouth (Steven & Corbin, 1939; Marine Biological Association, 1940*a*, *b*). The distribution of phosphates in the area in April 1938 has been described by Hickling (1938), and the phytoplankton distribution of the 1939 cruises has been examined in detail by Mare (1940).

In addition to the distribution of mackerel eggs and young stages in the Celtic Sea in 1937–9, the present paper gives an account of the spawning of the pilchard[1] and the distribution of certain zooplankton indicators—the *Sagitta* species of the area and *Muggiaea atlantica*. Temperature and salinity conditions are also described briefly; further detailed treatment of the hydrological data will be published at a later date.

The courses of the cruises and station numbers[2] are shown in Figs. 1 and 2. Details of station times and positions, and of numbers of organisms per haul are given in the Appendix (Table VI; pp. 124–32). For data of the French cruises, see Furnestin (1939*a*).

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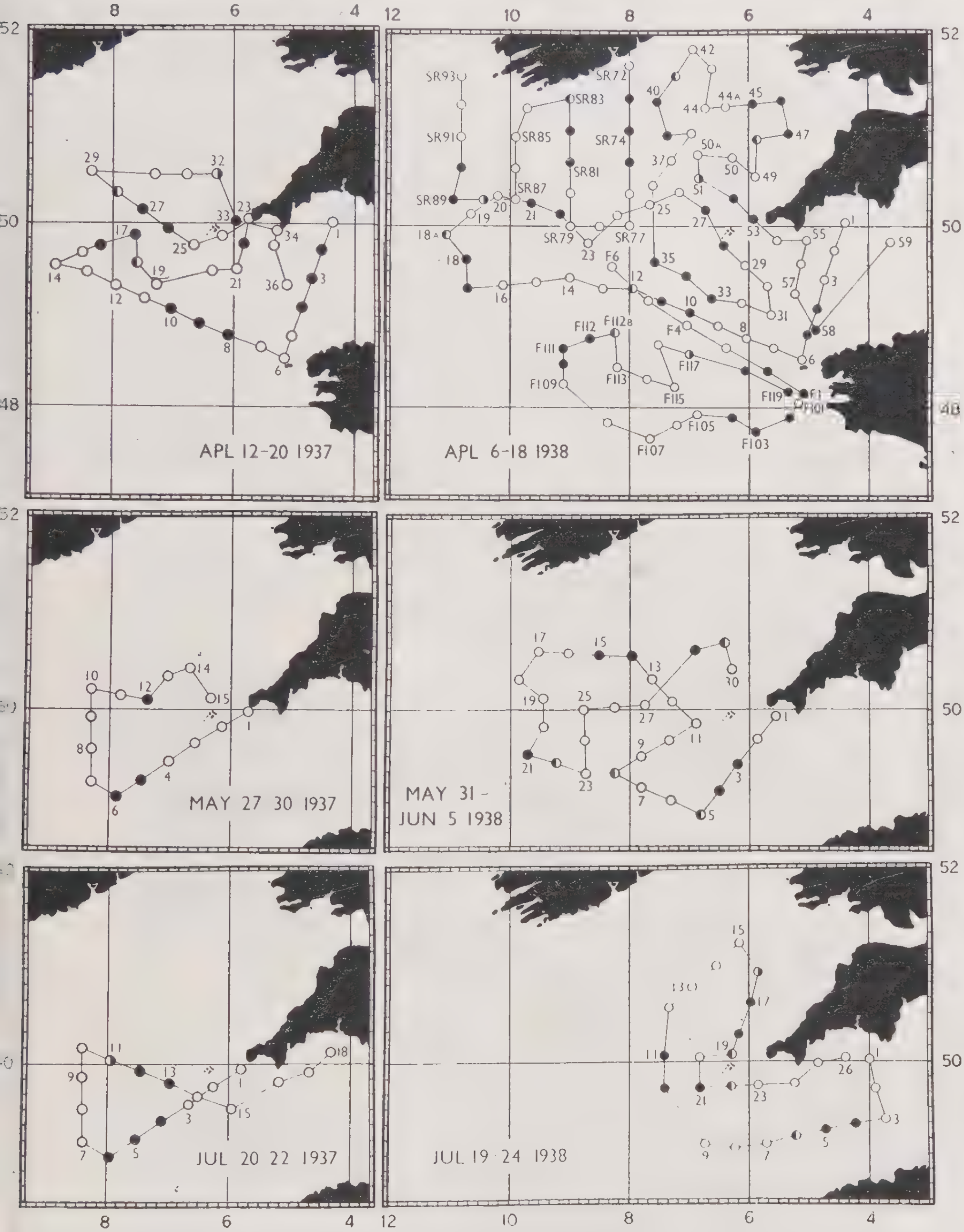
[1] Furnestin's paper (1945) on the biology of the Atlantic pilchard was received at the Plymouth Laboratory after completion of the present paper.

[2] In the text and figures, the station numbers of the *Muirchu* cruises are shortened by omitting the first two figures of the station number. Thus, Station SR 2872 reads SR 72. Full station numbers are given in Table VI with the last two figures printed in heavy type.


APL 12-20 1937
APL 6-18 1938
MAY 27 30 1937
MAY 31 - JUN 5 1938
JUL 20 22 1937
JUL 19 24 1938
8
6
4
12
10
8
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48
SR93
SR91
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SR87
SR85
SR83
SR81
SR79
SR77
SR74
SR72
F6
F4
F1
F101
F103
F105
F107
F109
F111
F112
F112B
F113
F115
F117
F119

Fig. 1. 1937 and 1938 cruises; station positions. Stations worked by the *Muirchu* have the prefix SR; those worked by the *Quentin Roosevelt* have the prefix F. Only the first six stations (F 1–F 6) of the first cruise of the *Quentin Roosevelt* are shown; all stations (F 101–F 119) of the second cruise are shown. ◐ dawn; ○ day; ◑ dusk; ● night.

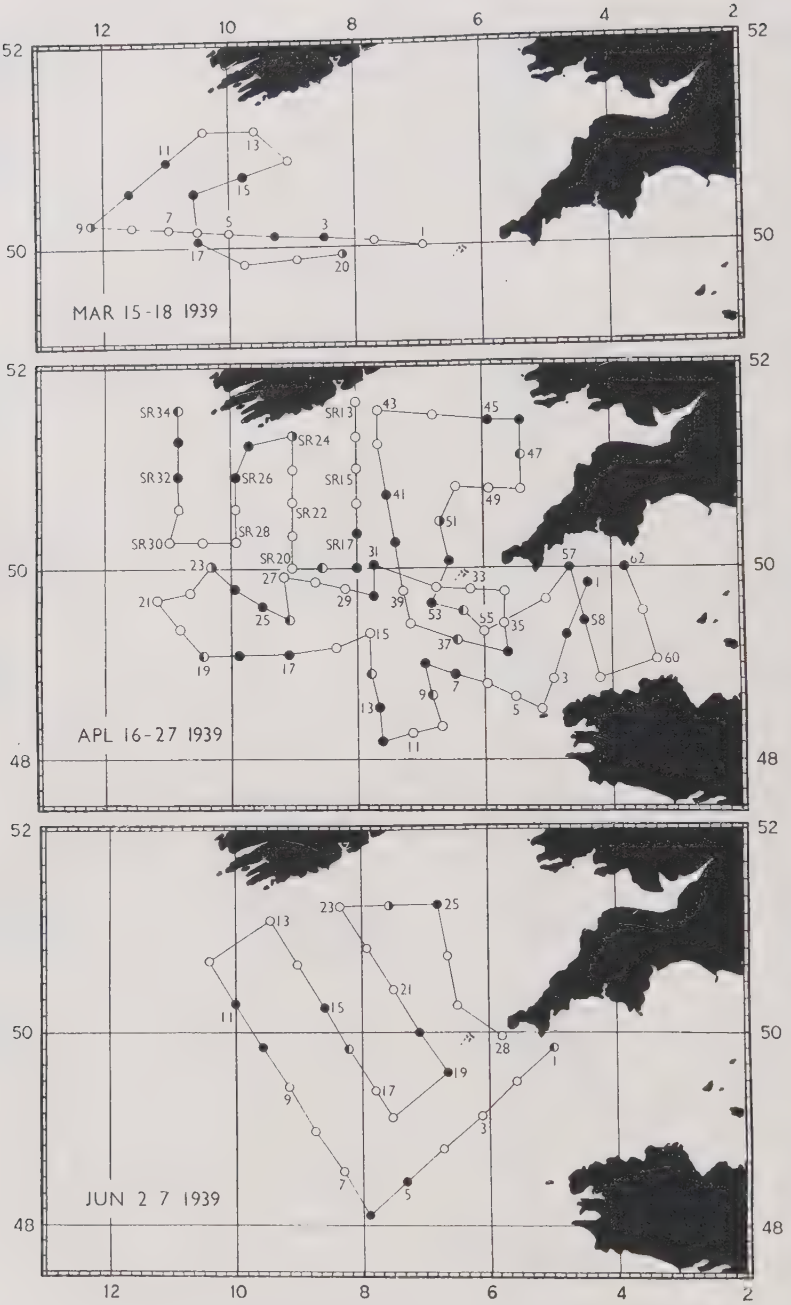
MAR 15-18 1939
APL 16-27 1939
JUN 2 7 1939
SR34
SR32
SR30
SR24
SR26
SR28
SR22
SR20
SR13
SR15
SR17
12
10
8
6
4
2
52
50
48

Fig. 2. 1939 cruises; station positions. Stations worked by the *Muirchu* have the prefix SR. ◐ dawn; ○ day; ◑ dusk; ● night.

Collection and Examination of Material

Throughout the cruises made from Plymouth and Eire, plankton was collected by half-hour oblique hauls of the 2 m. stramin ring-trawl. The method of fishing was the same as that described by Russell (1930, 1935*a*), but a slightly greater depth of water was sampled, the marks on the warp being at 10, 20, 35, 50 and 70 fm. (18, 36, 63, 91 and 126 m.) (Le Danois, 1939*a*). The use of a standard method of collection permits some degree of quantitative comparison of the results of different cruises and different years, but no more than broad comparisons can be made since stations were worked both in daylight and darkness during the cruises. On the *Quentin Roosevelt* cruises, hauls were made horizontally (15 min. at surface) or vertically (25–0 m. and 50–0 m.) with a 33 cm. 'petit filet type Boulogne' or a 1 m. 'grand filet Schmidt' (Furnestin, 1939*a*). The data are therefore not quantitatively comparable with those obtained by the oblique hauls of the 2 m. stramin ring-trawl, but are valuable as qualitative records. Water samples and temperature readings were taken with the Nansen-Petterson water-bottle.

All young fish caught in each haul were picked out for counting and identification. The fish-eggs in each haul were also picked out for counting and identification, or, in hauls where they were very numerous, the number was estimated by sampling.[1] The same methods were also used for the indicator species. The eggs were identified largely by inspection; the number dealt with was far too great to permit of identification of individual eggs by measurement of the diameter of the egg and of the oil globule. Inspection alone may perhaps be considered a somewhat uncertain means of identification, but it proves reliable after some experience in the recognition of different species of fish eggs has been acquired, and especially when used in combination with the certain identification characters provided by the chromatophore pattern of the embryo and the oil globule in the later development stages of the mackerel egg (Buchanan-Wollaston, 1911; Holt, 1893).

General Results

The Spawning of the Mackerel and the Distribution of the Pelagic Young Stages and the Spawning of the Pilchard

Before discussing the results of the present investigation, it will be of value to recall the existing records concerning the spawning of the mackerel in the seas around the south-west of the British Isles.

Matthias Dunn (1893) is remarkably accurate in his observations on the subject. He writes: '...the period of spawning...as a rule is in May and

---

[1] All totals obtained by sampling are indicated in Table VI by * after the number (e.g. 2450*); totals without this notation are exact counts.

June...and the spawning grounds...are in those waters covering the plateau of ground within the two hundred mile limit of our western and south-western shores.' Of the mackerel in the English Channel, he observes: 'They generally spawn late in June, but...I have known their spawning deferred so late as the 10th of August.' Allen (1897), summarizing the records of Cunningham (1890, 1892) for the Plymouth area, and of Holt (1892, 1893) and Green (1894) for the south-west coast of Ireland, gives the following as the chief spawning periods:

South-west of England (off Plymouth).	End of May to end of July.
South-west of Ireland.	May and June.

The records of mackerel young stages from Plymouth waters in the years 1906, 1908–9, 1913–14, 1917 and 1919 (Allen, 1917; Lebour, 1918; Clark, 1914, 1920) also led Clarke to observe that spawning in the area takes place from May to July, but he notes that, '...a later spawning period has been observed for some years, *vide* Lebour (1918) for the record of post-larvae in September 1917', and he concludes by giving the spawning period as May–August (Clark, 1920). Ehrenbaum (1923) quotes Allen, Cunningham, Holt and Green. Lissner (1939) gives the spawning period in the Channel and North Sea as (May), June and July, and for Ireland as (April), May, June and July. From records of the occurrence of mackerel young stages in the 2 m. ring-trawl plankton collections made throughout the year at Plymouth, Russell (1930, 1935*a*, 1936*b*, 1937, 1938*b*, 1939*a*, 1940) classifies the mackerel as a summer-spawner in Plymouth off-shore waters, noting however that 'the main spawning region is probably considerably further to the westward' (1926). Farran (1939) records very intense spawning to the south of Ireland in April 1938. Le Gall (1939) states: 'Dès Mars, aux accores du Plateau Continental Atlantique, on constate la présence d'œufs de maquereaux dans le plancton.... La ponte du maquereau débute donc vers mi-Mars à l'entrée occidentale de la Manche. Elle s'intensifie en Avril et en Mai (maximum), se poursuit en Juin, en Manche Occidentale. Nous avons pu l'observer jusqu'à la fin d'Août en Manche Orientale.' In a preliminary report of the present investigation, Steven & Corbin (1939) also state that spawning lasts from March until July or August, with a maximum from mid-April to mid-May, and occurs within the area of the Continental Shelf but mainly off-shore. This observation was based on a detailed examination of the 1937 material of the Plymouth investigation, together with a preliminary inspection of the plankton collections of 1938 and 1939. A full examination of all the material has now been completed and has revealed in considerable detail the locality and period of spawning of the mackerel population of the Celtic Sea in 1937–9. Probably the most outstanding feature of the survey is the similarity in each year of the numbers and locality of mackerel eggs and young stages, and of the sequence of changes with time in these two components of distribution.

Spawning begins in about the second week of March and continues until the end of July and into August. It increases very rapidly in intensity after the start and by mid-April reaches a peak which lasts until May. Thereafter it decreases more gradually, until by the end of July it is only very slight. This changing intensity of spawning is shown in Fig. 3 and Table I.

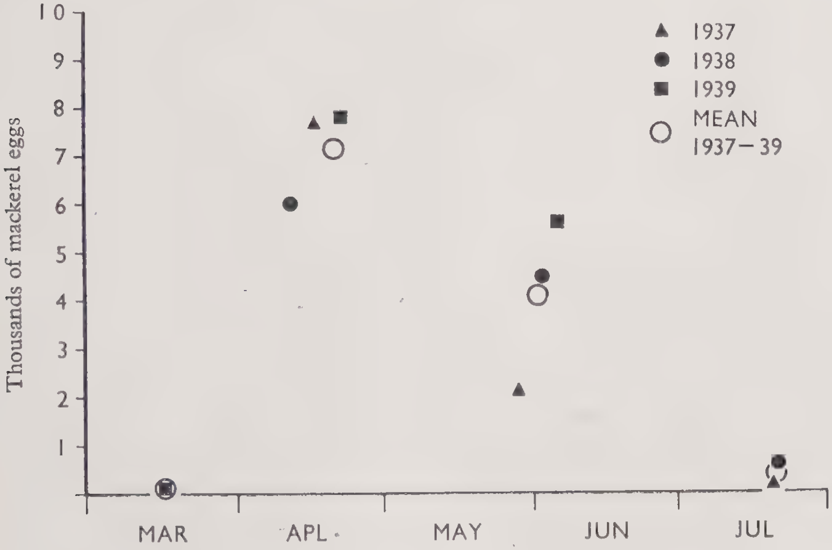

Fig. 3. Variation in intensity of spawning of the mackerel (data in Table I).

TABLE I. AVERAGE FOR EACH CRUISE OF THE TOTAL OF MACKEREL EGGS AT ALL STATIONS WHERE MORE THAN 100 WERE TAKEN

The number of stations from which the averages are obtained is shown in parentheses

	March	April	May–June	July
1937	No cruise	7659 (14)	2127 (10)	135 (1)
1938	No cruise	6003 (42)	4485 (23)	571 (7)
1939	118 (1)	7802 (38)	5660 (26)	No cruise
Mean 1937–9	118	7154	4090	353

Spawning takes place throughout the Celtic Sea during the period March to July. In the English Channel, and also in the Irish Sea, it is known to continue until August and probably in some years even until September, well after the main activity has finished in the Continental Shelf area. At the beginning of spawning in mid-March, the area is small and is situated well to the south-west of Ireland in the waters overlying the edge of the Continental Shelf (Fig. 8). By the mid-April peak, it has spread eastwards over the whole of the Celtic Sea, as far as the mouth of the English Channel and the entrances of the

St George's and Bristol Channels. There is little evidence that it extends into open oceanic waters beyond the 100 fm. line. The number of eggs, however, varies greatly in different parts of the area, and spawning is concentrated in two centres—to the west and south of the Celtic Sea. Of these, the outer western centre lying to the south of Ireland is the more extensive and contains the higher density of eggs. The inner southern centre covers a smaller area to the west of the Brest Peninsula and has a lower egg density. The two centres are shown in Figs. 4A, 5A and 9A by the contour enclosing all stations at which over 5000 mackerel eggs were taken. Between the centres spawning is not so intense, and outside them and the area immediately between them it is of still lower intensity, the number of mackerel eggs seldom exceeding 500 per haul. In April 1938 and 1939, there was a small isolated concentration of eggs off the mouth of the Bristol Channel; the intensity of spawning was lower than that of the two main centres but noticeably greater than in the surrounding areas. As the season advances, the locus of spawning moves farther east and north, and by the end of May there is very little spawning in the original locality of the outer April centre. But the continuation of it, shifted considerably north-eastwards, can be recognized in the spawning which occurs to the north-west of the Scilly Isles, between the north Cornish coast and the south-east coast of Ireland. The inner spawning centre of April is still present and has shifted only slightly to the north-east—towards the middle of the mouth of the English Channel. Its density of eggs in contrast to that of the outer centre is somewhat increased (Figs. 6A, 9A). Le Gall (1928*a*) draws attention to the gradual eastward and northward shift of spawning during April and May from the region south of Ireland, and he remarks on the presence at the end of May of two spawning areas towards the east—at the entrance to the St George's Channel (51° 18′ N., 7° 03′ W.) and some distance to the west of Ushant (48° 33′ N., 5° 50′ W.). The decrease in intensity of spawning and the eastward shift continue, and by mid-July no eggs are present to the west of Scilly. Their maximum numbers are little more than 1000 per haul in contrast to over 99,000 and 45,000 in April (1938, 1939). The occurrence of the larger hauls in the eastern part of the July spawning area indicates that the movement of spawning eastwards along the Channel and northwards into the Irish Sea still continues (Figs. 4C, 7A). In this connexion, Scott's records from the Irish Sea are especially valuable as they cover a considerable period of years. He found mackerel eggs only once in the northern area (south-west of the Isle of Man) during the years 1907–13. Farther south they were more numerous and he states that 'the eggs are not uncommon in the Cardigan Bay plankton at the beginning of July and it is possible that the majority of fish that arrive in the central area spawn on the way up from the south'. In support of this, he found that mackerel caught off Walney (north Lancashire) early in July (1901–12) were invariably in a spent condition (Scott, 1913, 1914*a*, *b*).

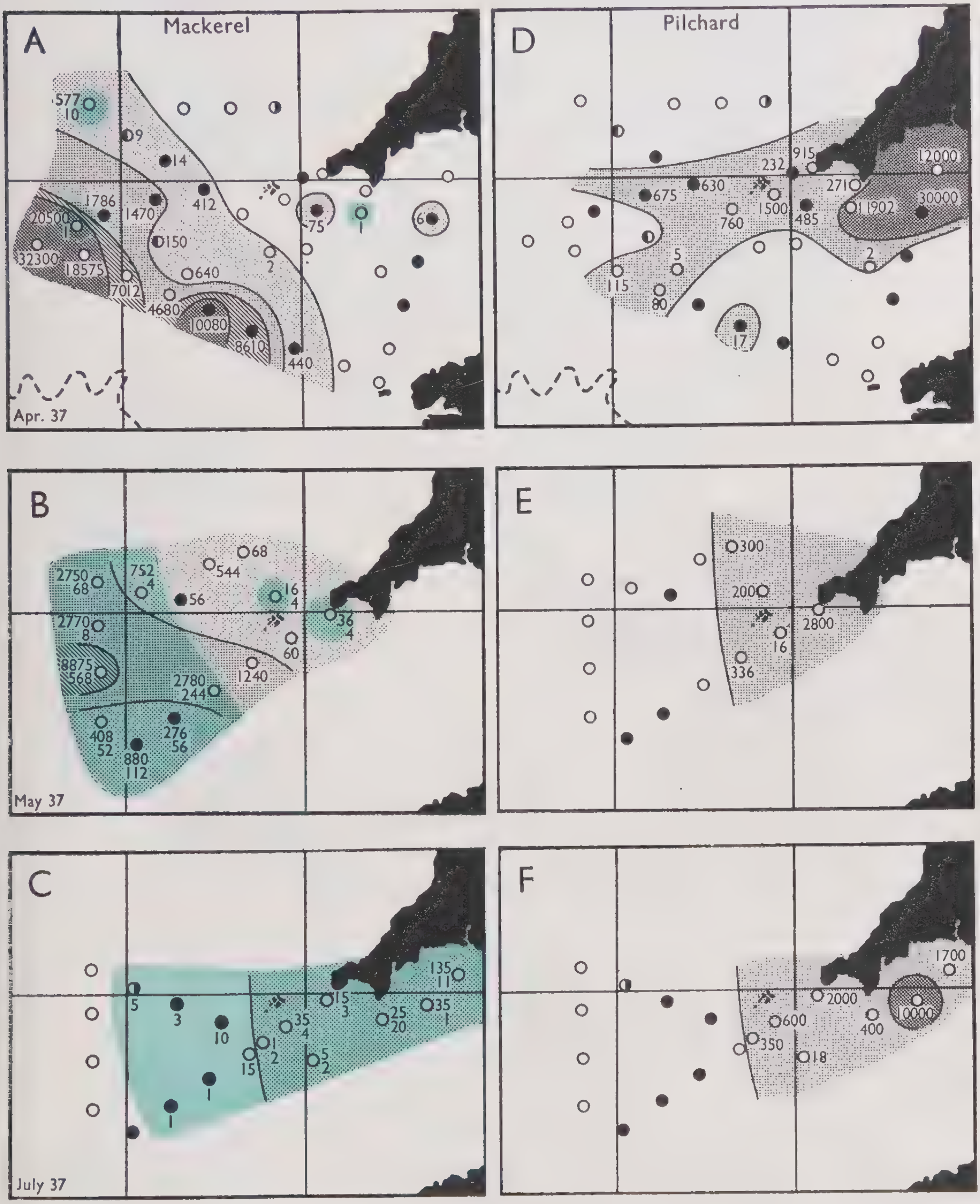
A
Mackerel
577
10
9
14
1786
1470
412
20500
1
150
75
1
6
32300
18575
7012
640
2
4680
10080
8610
440
Apr. 37
D
Pilchard
915
232
12000
630
675
271
30000
1500
11902
760
485
5
2
115
80
17
B
68
544
2750
68
752
4
56
16
4
2770
8
36
4
60
8875
568
1240
2780
244
408
52
276
56
880
112
May 37
E
300
2000
2800
16
336
C
135
11
5
3
10
15
3
35
4
25
20
35
1
1
2
15
5
2
1
1
July 37
F
1700
2000
10000
600
400
350
18

Fig. 4. Distribution of mackerel eggs (1–1000, 1001–5000, 5001–10,000, >10,000) and young stages (blue areas) (A, B and C), and pilchard eggs (1–5000, >5000) (D, E and F) in the Celtic Sea in April, May and July 1937. Figures refer to the numbers of eggs and young stages at each station. The broken line in this and succeeding figures indicates the 100 fm. contour.

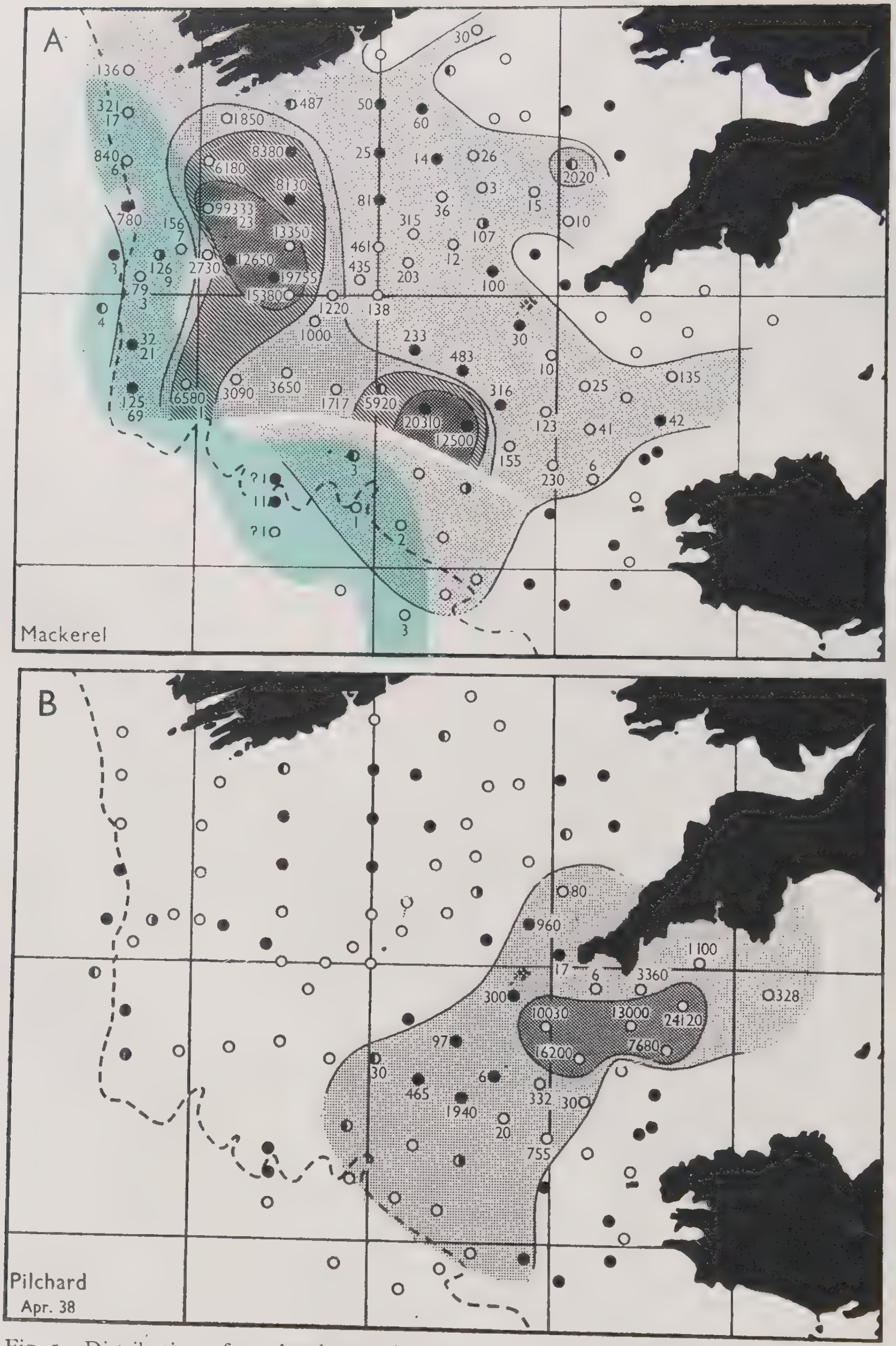
A
30
136
321
17
487
50
1850
60
840
6
8380
6180
25
14
26
2020
8130
99333
23
81
3
36
15
780
156
7
13350
315
107
10
461
12
3
126
9
2730
12650
435
203
19755
100
79
3
15380
1220
138
4
1000
233
30
32
21
483
10
3650
3090
1717
25
135
125
69
6580
1
5920
316
42
20310
123
41
12500
155
3
230
6
?1
11
1
2
?10
3
Mackerel
B
80
960
1100
17
6
3360
300
328
10030
13000
24120
97
7680
16200
30
6
465
332
30
1940
20
755
Pilchard
Apr. 38

Fig. 5. Distribution of mackerel eggs (1–1000, 1001–5000, 5001–10,000, > 10,000) and young stages (blue area) (A), and pilchard eggs (1–5000, > 5000) (B) in the Celtic Sea in April 1938. Figures refer to the numbers of eggs and young stages at each station. Numbers of mackerel eggs and pilchard eggs at Sts. F 101–F 119 are not given (Furnestin, 1939*a*).

The changes in numbers and distribution of mackerel young stages[1] in the Celtic Sea are very similar to those of the eggs. None occurred in March 1939, and there appear to be no previous records of any being taken in the area as early as March. In the third week of April, small numbers of larvae and post-

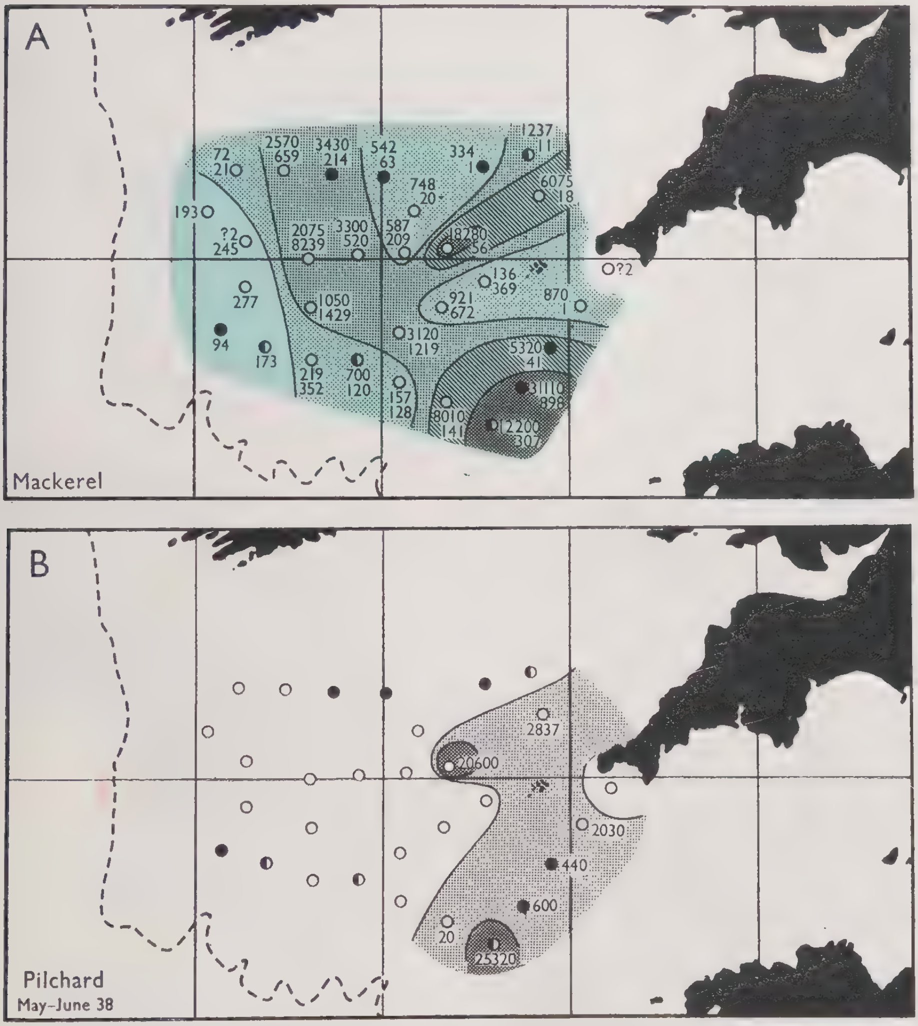
A
72
210
2570
659
3430
214
542
63
334
1
1237
11
6075
18
748
20
193
?2
245
2075
8239
3300
520
587
209
18280
56
136
369
?2
870
1
921
672
277
1050
1429
94
173
3120
1219
5320
41
219
352
700
120
157
128
31110
898
8010
141
12200
307
Mackerel
B
2837
20600
2030
440
600
20
25320
Pilchard
May–June 38

Fig. 6. Distribution of mackerel eggs (1–1000, 1001–5000, 5001–10,000, > 10,000) and young stages (blue area) (A), and pilchard eggs (1–5000, > 5000) (B) in the Celtic Sea in May–June 1938. Figures refer to the numbers of eggs and young stages at each station.

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[1] The material consists of 22,203 specimens; the largest measures 21 mm. (including tail) and may be regarded as past the post-larval stage since there is silvery pigment over most of the body and the finlets are developed on the caudal peduncle.

larvae are present in the plankton of the outer margin of the area—beyond the main spawning centres and towards the western and south-western edge of the Continental Shelf (Figs. 5 A, 9 A). The numbers caught in April 1938 and 1939

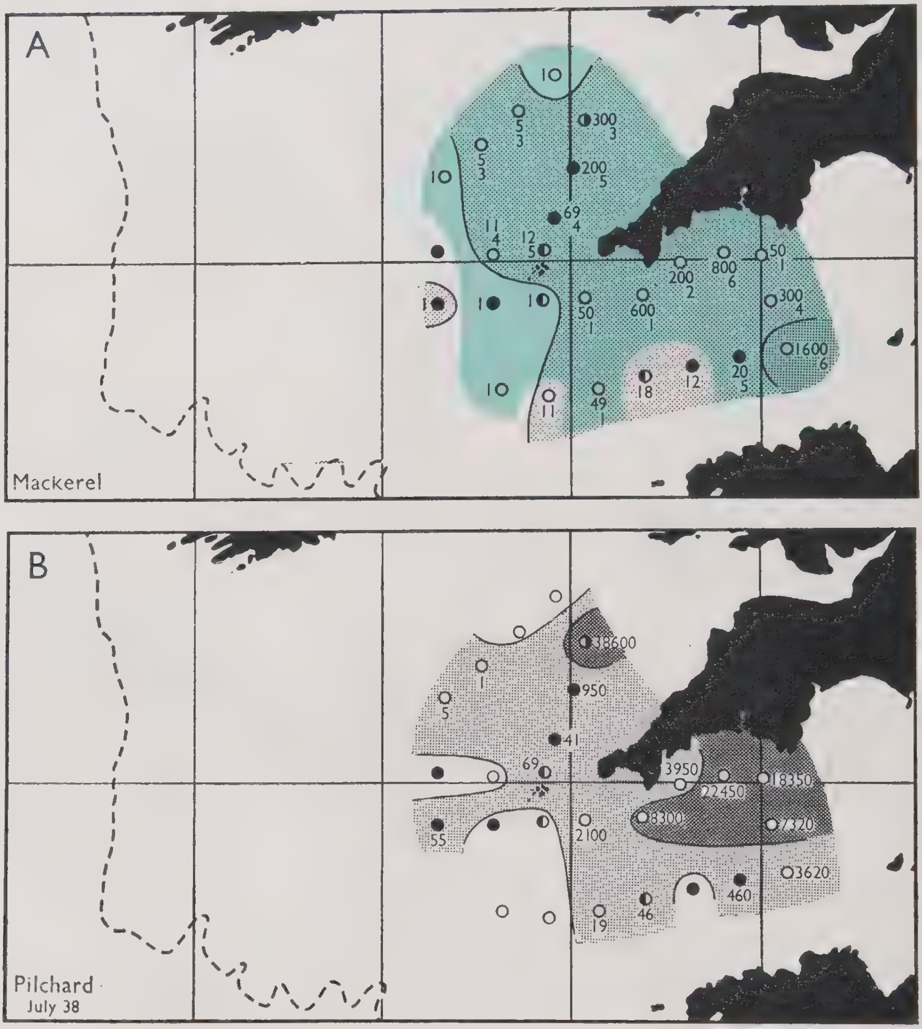
A
Mackerel
10
5
3
300
3
200
5
69
4
11
4
12
5
10
10
1
1
1
50
1
200
2
800
6
50
1
600
1
300
4
1600
6
11
49
1
18
12
20
5
10
B
Pilchard
July 38
38600
1
5
950
41
69
3950
22450
18350
8300
7320
55
2100
3620
460
46
19

Fig. 7. Distribution of mackerel eggs (1–1000, 1001–5000) and young stages (blue areas) (A), and pilchard eggs (1–5000, > 5000) (B) in the Celtic Sea in July 1938. Figures refer to the numbers of eggs and young stages at each station.

in this region were almost all under 100 per haul. Le Gall (1928*a*) records young stages in April to the south of Ireland in the region of 50° 50′ N., 10° 00′ W., (18–26 April 1927). They do not occur, or are present in very small numbers only, on the landward side of the spawning centres—in the central, northern and eastern areas of the Celtic Sea. In April 1939, three specimens were taken close to the small concentration of eggs off the mouth of the Bristol Channel. By the end of May and beginning of June, they are present throughout the Celtic Sea and are particularly abundant in the central area stretching from south-west Ireland to the Brest Peninsula (Figs. 4B, 6A, 10A). The largest haul contained 8239 specimens (St. 25, June 1938, day haul). They are less numerous towards the edge of the Continental Shelf, and also eastwards towards the English Channel and northwards towards the entrance to the Irish Sea. They are only occasionally taken at Plymouth in May but occur regularly there in small numbers in June (Allen, 1917; Lebour, 1918; Clark, 1914, 1920; Russell, 1930, 1935*a*, *et seq.*), and Clark (1914) observes that 'it is highly probable that the early stages occur in greater numbers much further out than the area investigated'. The area of abundance of young stages bears the same relationship to the spawning centres at this time of year as did the area of occurrence of young stages in April. It is situated beyond them—towards the edge of the Continental Shelf. By July they are much less abundant, even fewer than in April. Their continued move to the north and east is still evident and they are no longer present in the central area of the Celtic Sea to the west of 8° W. where previously, at the beginning of June, they were so numerous (Figs. 4C, 6A). Table II shows the average total of mackerel young stages taken on each cruise. The maximum at the end of May and beginning of June stands out clearly. At Plymouth, Russell (1930, 1935*a*, *et seq.*) finds a maximal occurrence of young stages in July. They continue to be present in the plankton in August in the majority of years, and even until September (Lebour, 1918 and Russell, 1935*a*; records in September 1917 and 1930, 1931 and 1932). The figures in Table II show that the average for the July cruises (1937, 6; 1938, 2·8) is in close agreement with the July monthly average at Plymouth (period 1930–9; July average, 9).

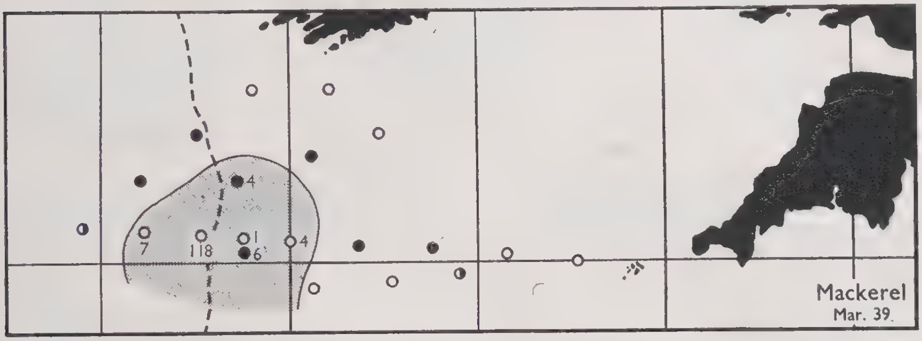

Fig. 8. Distribution of mackerel eggs in the Celtic Sea in March 1939. Figures refer to the number of eggs at each station. No young stages were taken.

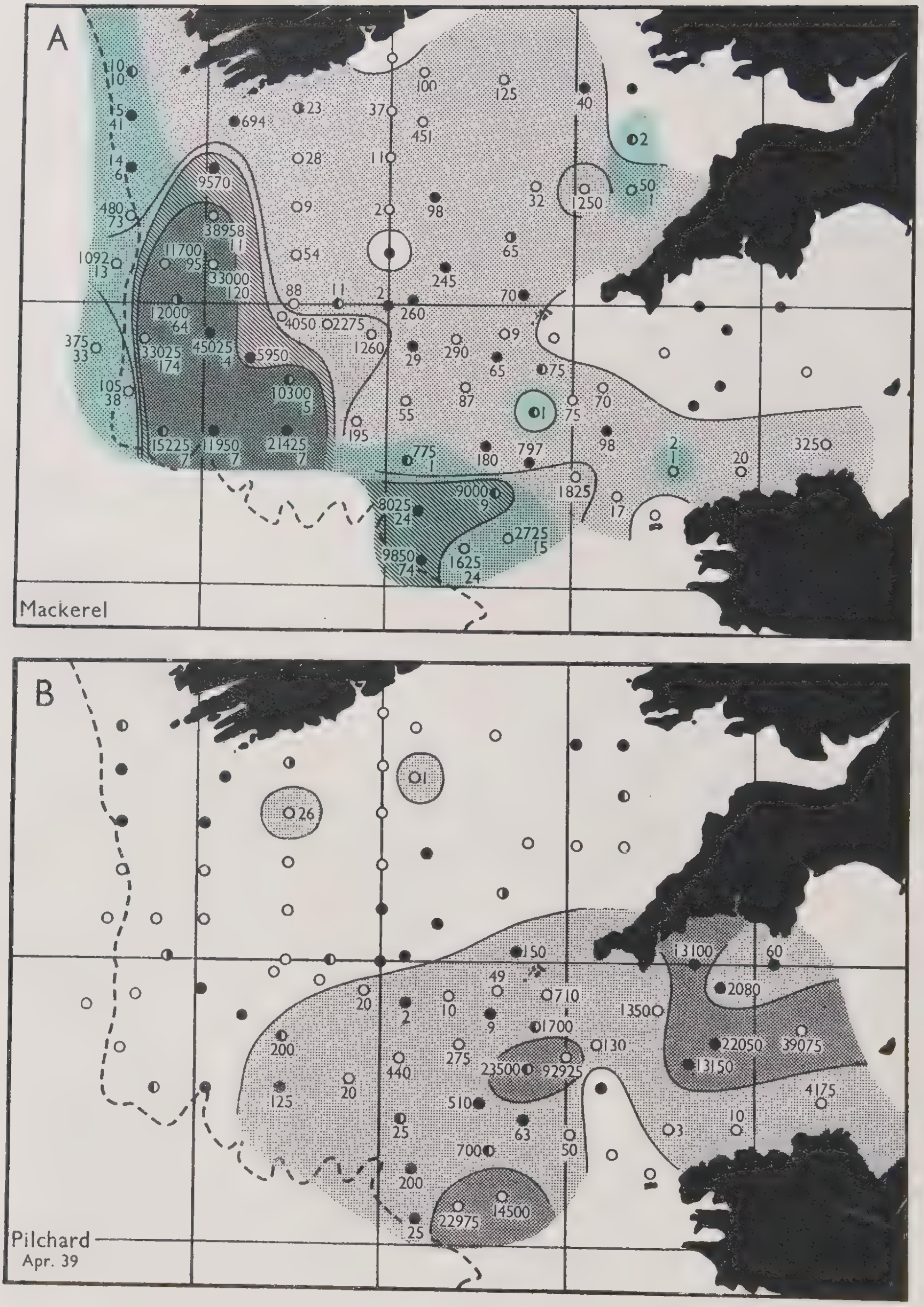
A
Mackerel
10
10
15
41
14
6
480
73
1092
13
375
33
105
38
694
23
28
9
54
9570
38958
11
11700
95
33000
120
12000
64
33025
174
45025
4
5950
10300
5
15225
7
11950
7
21425
7
88
11
2
4050
2275
1260
195
37
11
2
100
451
98
245
260
29
290
55
87
125
32
65
70
9
65
75
75
70
40
2
50
1
1250
1
775
1
180
797
98
9000
9
8025
24
9850
74
1625
24
2725
15
1825
17
2
1
20
325
B
Pilchard
Apr. 39
26
1
150
13100
60
2080
49
710
1350
20
2
10
9
1700
200
440
275
130
22050
39075
13150
23500
92925
125
20
510
4175
25
63
10
3
700
50
200
22975
14500
25

Fig. 9. Distribution of mackerel eggs (1–1000, 1001–5000, 5001–10,000, > 10,000) and young stages (blue areas) (A), and pilchard eggs (1–5000, > 5000) (B) in the Celtic Sea in April 1939. Figures refer to the numbers of eggs and young stages at each station.

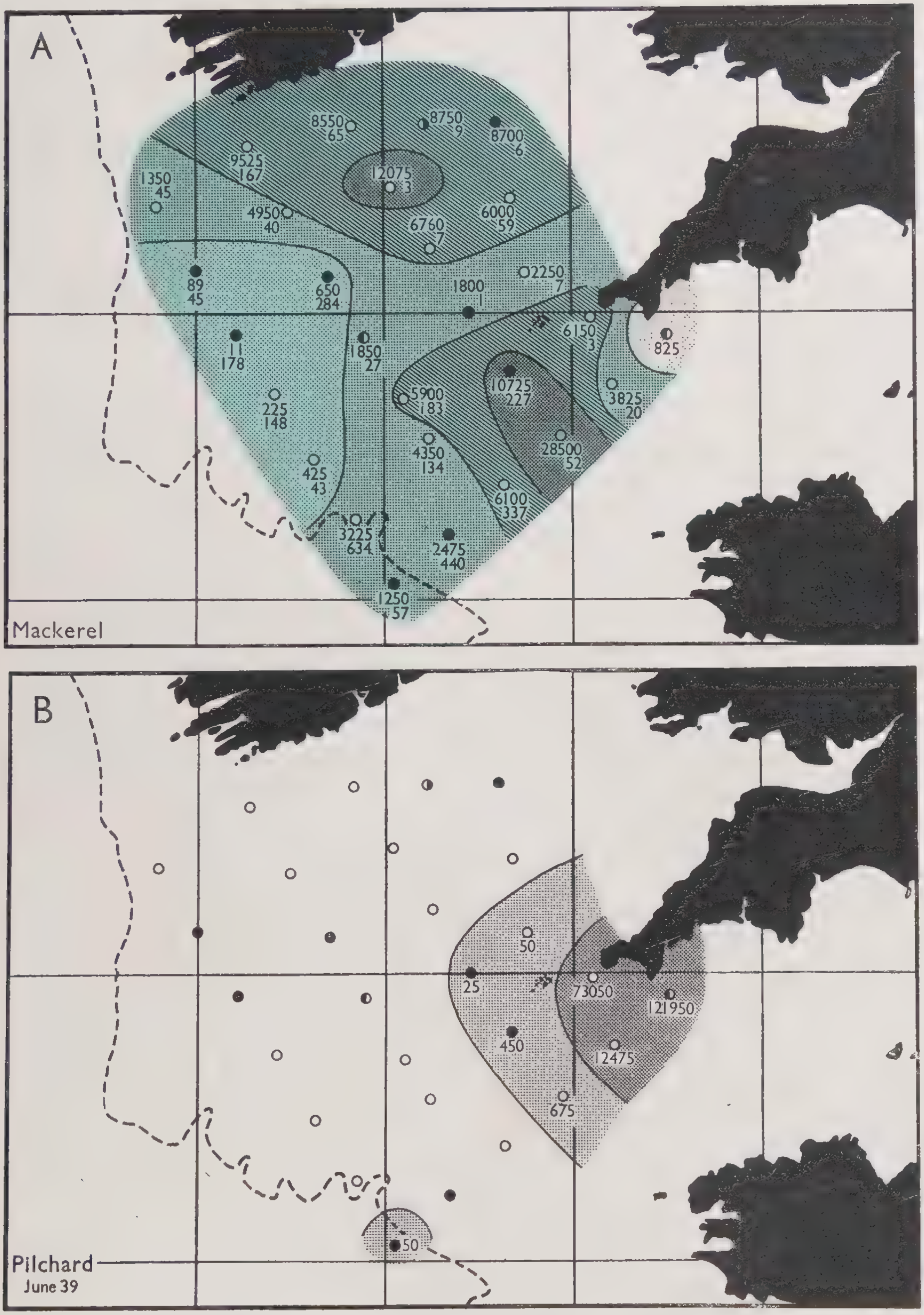
A
8550
65
8750
9
8700
6
9525
167
1350
45
12075
3
4950
40
6000
59
6760
7
89
45
650
284
1800
1
2250
7
11
178
1850
27
6150
3
825
5900
183
10725
227
3825
20
225
148
4350
134
28500
52
425
43
6100
337
3225
634
2475
440
1250
57
Mackerel
B
50
25
73050
121950
450
12475
675
50
Pilchard
June 39

Fig. 10. Distribution of mackerel eggs (1–1000, 1001–5000, 5001–10,000, > 10,000) and young stages (blue area) (A), and pilchard eggs (1–5000, > 5000) (B) in the Celtic Sea in June 1939. Figures refer to the numbers of eggs and young stages at each station.

TABLE II. AVERAGE FOR EACH CRUISE OF THE TOTAL OF MACKEREL YOUNG STAGES

The number of stations at which they occurred is shown in parentheses

	March	April	May–June	July
1937	No cruise	3 (3)	112 (10)	6 (13)
1938	No cruise	14 (11)	575 (29)	2 (21)
1939	Nil	33 (26)	118 (27)	No cruise
Mean 1937–9	Nil	17	268	4

Among the plankton collected during 1937–9, some of the hauls contained pilchard eggs. These were counted in order to obtain information on the spawning area of the Cornish pilchard. Lebour (1921) records that the pilchard spawns some distance off shore in the Plymouth area—particularly in the region of the Eddystone, and that spawning lasts from mid-March until October, probably continuing into November, with a maximum from June to August. Le Gall (1928*b*) states that spawning takes place within the area: Scilly–Ushant–Cap de la Hague–Start Point. Furnestin (1939*a*) found eggs at the end of March and beginning of April, 1938, in the Channel mouth, to the south of the Scilly Isles and to the west of the Brest Peninsula as far as 8° 14′ W., and he concludes that spawning occupies a fairly wide area over the Continental Shelf. The distribution of pilchard eggs observed during the present investigation confirms this (Figs. 4–7, 9 and 10). Spawning takes place in the mouth of the English Channel and over a considerable area to the west as far as 8° W. In April 1939, it extended to 9° W. North of the Scilly Isles it is confined to the area along the Cornwall coast. It does not appear to occur to any great extent to the south and south-east of Ireland; a single egg was taken to the south-west of Ireland in March 1938 (50° 42′ N., 10° 00′ W.; St. 9; Furnestin, 1939*a*) and twenty-seven were taken off the south coast in April 1939 (Sts. 42 and SR. 23). The eastern limit of spawning is not indicated by the 1937–9 records and it is possible that spawning may occur throughout the length of the Channel and in the southern North Sea. Furnestin (1939*b*) observed considerable spawning from May until August (1931–4), with a maximum in June, in the region of the *Sandettié* lightship in the northern entrance to the Straits of Dover (51° 13′ N., 1° 53′ E.). He also obtained numerous eggs in three plankton hauls taken to the east of Beachy Head (0° 05′ W., 50° 40′ N.) in mid-June (10th–12th, 1938). He concludes that these spawning areas are probably continuous with that at the western end of the Channel. The southern limit of spawning was not conclusively determined on the 1937–9 cruises, but it seems very unlikely that it lies beyond the edge of the Continental Shelf. The lack of stations inside the Channel mouth prevents as comprehensive a survey of the distribution of pilchard eggs throughout each year as was possible with mackerel eggs. It is, however, evident that the main pilchard spawning area lies at the western entrance of the English

Channel, although intense spawning activity also takes place farther to the west, beyond the Channel mouth. In June 1938 and April 1939 two small concentrations, in which eggs were quite as numerous as in the main spawning area, occurred outside the mouth of the Channel (Figs. 6B, 9B). The distribution of pilchard eggs at the end of May and beginning of June, and in July, indicates that the spawning area does not extend in these months quite so far west as in April. Its western limit lies nearer to 7° W. than to 8° W. The average for each cruise of the total of pilchard eggs at all stations where more than 100 were taken is shown in Table III.

TABLE III. AVERAGE FOR EACH CRUISE OF THE TOTAL OF PILCHARD EGGS AT ALL STATIONS WHERE MORE THAN 100 WERE TAKEN

The number of stations from which the averages are obtained is shown in parentheses

	April	May–June	July
1937	4957 (12)	934 (4)	2508 (6)
1938	4474 (14)	8687 (6)	6895 (10)
1939	10,611 (22)	34,909 (5)	No cruise
Mean 1937–9	7542	21,798	6895

The 1937 averages show a maximum in April and a minimum at the end of May. In 1938 and 1939, however, the maximum occurred on the May–June cruise each year. It is possible that the irregularity of the 1937 averages may to some extent be due to the use of a smaller net on the May cruise and to the fact that only the fringe of the pilchard spawning area was worked. Pilchard eggs have been a constant and especially marked feature of the Plymouth plankton catches. They occur each year from April to November, with records in March in 1936 and in December in 1931, 1938 and 1939 (Russell, 1935*a*, 1936*b*, *et seq.*). These records have a maximum in June which Hickling (1945) has shown to be coincident with the maximum occurrence of spawning fish and with maxima in gonad weight, feeding activity and growth of the adult fish. Hickling's samples were obtained in the years 1936–8. This evidence strengthens the probability that the 1938 and 1939 averages are the truer reflexion of the changes in intensity of spawning and that the figures for 1937 are not representative.

The relationship of the mackerel and pilchard spawning areas is apparent in Figs. 4–7, 9 and 10. In April the main pilchard spawning in the Channel mouth takes place in an area containing few or no mackerel eggs (Figs. 4, 5, 9). As the season advances, the north-easterly shift of the mackerel spawning centres brings them nearer to those of the pilchard, and by the end of May and early June, there is considerable overlapping. This was particularly evident in May–June of 1938 when the spawning centres of the two species occupied the same areas (Fig. 6). The continued movement of the spawning of the mackerel eventually completes the overlapping of the total spawning areas of the two species—not merely of the centres. This can be seen from the distribution of mackerel and pilchard eggs in July 1937 and 1938 (Figs. 4 C, F, 7). The overall spawning areas were identical and it is noteworthy that the largest hauls of mackerel eggs were taken to the eastward in exactly those areas of maximal pilchard spawning activity.

Comparison of the distribution of phytoplankton in 1939 (Mare, 1940) and of mackerel and pilchard eggs gives no indication of any close relationship. In March, there was very little phytoplankton in the region where mackerel spawning was just starting. In April, both mackerel spawning centres were situated in areas of medium phytoplankton density. In May–June, the northern spawning centre was in an area of particularly sparse phytoplankton, while the southern centre lay in the region of greatest phytoplankton density. It must be noted, however, that in May–June phytoplankton production was very low throughout the area of the cruise and at its highest approached only the lower values of April. The main pilchard spawning areas in April were located largely in areas of dense phytoplankton, whereas in May-June, they were in an area of sparse phytoplankton. Far more data are required for further examination of the possibility of any correlation between the spawning of either the mackerel or pilchard and the distribution of phytoplankton.

The salinity and temperature observations of the 1937–9 cruises provide opportunity for examining the possibility of a relation between these factors and the distribution of the spawning centres of the mackerel and pilchard. Le Gall (1939) writes of the mackerel: 'Les déplacements des bancs à l'entrée occidentale de la Manche et à l'entrée sud de la Mer d'Irelande paraissent se faire principalement suivant les axes transgressifs caractérisés par une température et une salinité élevées (salinité supérieure a 35 °/₀₀ et température variant de 10° a 15° suivant l'époque de l'année). La ponte se fait également dans les eaux transgressifes: les œufs et les larves de maquereaux étant nettement plus abondants dans les pêches planctoniques faites dans ces eaux.' Furnestin (1939*a*) also notes: 'la présence d'œufs et de larves de maquereaux semble être strictement limitée aux régions où se manifestent les trois grandes poussées transgressives'; and further, that it was only at stations of salinity near to or above 35·50 °/₀₀ that mackerel eggs and young stages were taken on the *Quentin Roosevelt* cruises in 1938. Farran (1939) on the other hand observes that at the western stations of the *Muirchu* cruise of April 1938 where salinities exceeded 35·60 °/₀₀, the numbers of mackerel eggs were low, in contrast to their particular abundance farther east in water of lower salinity. Of the spawning area of the pilchard Furnestin (1939*a*) remarks that it is 'en rapport étroit avec le mouvement général de la transgression atlantique sur le Plateau Continental. En effet, les différentes stations où nous avons trouvé des œufs de sardine sont situées sensiblement dans l'axe de la transgression. Ailleurs, dans les eaux continentales, nous n'en avons pas trouvé'. According to Fage (1920), the spawning and larval development of the pilchard in the

English Channel require a temperature of above 12° C.[1] and below 15° C. and he records a mean salinity of 35·27 $^{0}/_{00}$ during the spawning period, May–November. Le Gall (1928*b*) notes, however, that at one of the *Thor* stations[2] in the northern half of the Channel mouth, pilchard eggs were taken in a surface haul in water of 9·90° C., and he concludes that the pilchard in the Channel mouth area certainly spawns in temperatures below 12° C.

Table IV shows the mean temperature and salinity of the upper 25 m. of water in the mackerel and pilchard spawning centres in 1937–9 (means of all stations at which more than 5000 eggs were taken). Since there were indications of marked thermal stratification at 25 m. in May–June 1939 and July 1938, temperatures at surface and 5 m. only have been included; salinity means, however, include the values at 25 m. as vertically homohaline conditions extended to this depth. Mackerel spawning was much reduced (maximum, 1600 eggs) by July in 1938, although pilchard spawning was still very intense (maximum, 38,600 eggs); in order therefore to obtain as valid a comparison as

TABLE IV. MEAN TEMPERATURE AND SALINITY OF THE UPPER 25 M. OF WATER IN THE MACKEREL AND PILCHARD SPAWNING CENTRES

The number of stations from which the means have been calculated is shown in parentheses

	Salinity $^{0}/_{00}$		Temperature ° C.	
	Mackerel	Pilchard	Mackerel	Pilchard
April 1937	35·36 5, 25 m. (4)	35·18 5, 25 m. (2)	10·50 5, 25 m. (4)	9·51 5, 25 m. (2)
April 1938	35·35 0, 5, 25 m. (12)	35·36 0, 5, 25 m. (4)	10·27 0, 5, 25 m. (12)	10·07 0, 5, 25 m. (4)
April 1939	35·50 0, 5, 25 m. (14)	35·34 0, 5, 25 m. (5)	11·44 0, 5, 25 m. (14)	10·86 0, 5, 25 m. (5)
May–June 1939	35·15 5, 25 m. (7)	35·26 5, 25 m. (1)	14·63 5 m. (7)	11·42 5 m. (1)
July 1938	35·18 0, 5, 25 m. (3)	35·22 0, 5, 25 m. (5)	15·52 0, 5 m. (4)	15·70 0, 5 m. (6)

TABLE V. TEMPERATURE AND SALINITY RANGES IN THE MACKEREL AND PILCHARD SPAWNING CENTRES

Depths and number of stations as in Table IV above

	Salinity $^{0}/_{00}$		Temperature ° C.	
	Mackerel	Pilchard	Mackerel	Pilchard
April 1937	35·35–35·38	35·03–35·43	10·30–10·62	9·42– 9·71
April 1938	35·25–35·49	35·30–35·39	9·95–11·12	9·73–10·29
April 1939	35·33–35·58	35·10–35·52	10·49–12·30	10·27–11·80
May–June 1939	34·51–35·49	35·26–35·27	13·22–15·42	11·42
July 1938	35·06–35·36	35·06–35·36	14·16–16·30	14·16–16·30
Extreme range all cruises:	34·51–35·58	35·03–35·52	9·95–16·30	9·42–16·30

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[1] Le Gall (1928*b*, p. 23) erroneously quotes this as 14° C.

[2] Fage (1920, p. 36); St. 31, 7 May 1906, 49° 45′ N., 4° 42′ W.; 20 pilchard eggs.

possible of the conditions in the spawning areas of the two species, the means of temperature and salinity for July 1938 have been calculated from the values at all stations where more than 100 mackerel eggs and more than 500 pilchard eggs were taken. Table V shows the ranges of temperature and salinity occurring in the spawning centres of the two species.

Considering first the means, it is apparent that as the season advances, conditions of reduced salinity and increased temperature are encountered in the mackerel spawning centres. In the pilchard spawning centres, salinities remain almost constant from April to July, with an indication of a slight diminution during this period, while temperatures rise from rather lower to slightly higher values than in the mackerel spawning centres. As a corollary to the above, the range of salinity throughout the period April–July, as well as the range in each month, is noticeably greater in the mackerel than in the pilchard spawning centres, while the greater temperature range occurs in the pilchard spawning centres. It has previously been noted that mackerel spawning in July is much diminished. In making any inference from the above figures, it would therefore be more correct to exclude from consideration the conditions pertaining in July in the mackerel spawning area. This was, however, exactly coincident with the pilchard spawning area, so that in fact, the July conditions were common to the spawning areas of both species. Moreover, the above remarks apply if the July conditions in the mackerel spawning area are discounted.

In April 1937, the mackerel spawning centres were entirely confined to water of salinity $>35{\cdot}3\,^{0}/_{00}$, but it must be noted that this cruise was not as extensive as the April cruises of 1938 and 1939. In April 1938, an intrusion of saline water ($>35{\cdot}5\,^{0}/_{00}$) lay between the outer and inner spawning centres, where the intensity of spawning was only moderate by comparison with that of the centres. In April 1939, the two mackerel spawning centres were largely situated in water of salinity $>35{\cdot}4\,^{0}/_{00}$. In May–June 1939, the southern mackerel spawning centre occurred in salinities varying between $35{\cdot}26\,^{0}/_{00}$ and $35{\cdot}49\,^{0}/_{00}$, while the values in the northern centre were all lower than $35{\cdot}2\,^{0}/_{00}$. These figures show the very considerable range of salinity in which intense mackerel spawning activity occurs and point to the somewhat doubtful value of ascribing salinity 'limits' to the spawning areas of the mackerel. It is evident that the shift of spawning during the season brings about the extent of this range to a greater degree than actual changes in salinity itself at one place.

The Distribution of the Sagitta *species and of* Muggiaea atlantica *in Relation to Hydrological Conditions*

Before discussing the distribution of some of the zooplankton indicator species observed during the present investigation, it will be convenient to examine briefly the hydrological data obtained on the cruises of April 1937, 1938 and 1939, June 1939 and July 1938. Further details are given on pp. 109–117. In April 1937, 1938 and 1939 salinities were vertically homohaline generally. The disposition of the isohalines in April and July 1938 and in April and June (upper 25 m.) 1939 is in general agreement with the conception of an anti-clockwise or cyclonic circulation of the waters in the eastern part of the Celtic Sea, as described by Matthews (1914), Harvey (1925, 1929, 1930), Lumby (1925) and others. Medium salinity water (35·3–35·4 °/₀₀), probably derived from the salt water (> 35·5 °/₀₀) lying on the edge of the Continental Shelf to the west of the Brest Peninsula, extended northwards across the mouth of the English Channel and continued through the Land's End–Scilly Channel. Travelling along the north Cornish coast, it was turned west by the course of the circulation in the region of the Bristol Channel, then south-west and finally south, having now become considerably diluted and indistinguishable in salinity from the low salinity tongue (< 35·2 °/₀₀) forming the outer western south-flowing component of the circulation. In April 1937 conditions were rather different from the above. Very low salinity water (< 35·1 °/₀₀) extended from Ushant to the southern tip of the Cornish Peninsula, blocking the Channel mouth and separating medium salinity water (> 35·3 °/₀₀) in the neighbourhood of Plymouth from water of similar salt content to the west of the Channel mouth.

Attention has been drawn to the bearing of this circulation on the biology of the south-western area and its importance as a distributing agent of plankton organisms by the work of Gough (1905), Russell (1935*b*, 1936*a*, *c*, 1939*b*), Mare (1940), Corbin & Panikkar (1942).

The distribution on the 1937–9 cruises of *Sagitta elegans*, *S. setosa*, *S. serratodentata* and *S. lyra*, and of the siphonophore *Muggiaea atlantica* is described on pp. 97–109. Russell (1935*b*, 1936*a*, *c*, 1939*b*) has shown the value of plankton organisms, particularly *Sagitta elegans*, *S. setosa* and *S. serratodentata*, as indicators of water movements in the Celtic Sea. He found that *S. setosa* is associated with Channel water, *S. elegans* with mixed oceanic and coastal water in the area of the cyclonic swirl, and that *S. serratodentata*, a purely oceanic species, occurs in typical *elegans* water in years of strong Atlantic in-flow into the Channel. Water also enters the Channel mouth from the south-west. It may be warm and of purely oceanic origin with a characteristic macroplankton indicator community, which does not, however, carry any *Sagitta* species (Russell, 1935*b*, 1939*b*), or it may be low salinity water entering close round Ushant (Poole & Atkins, 1929). The 1937–9 records clearly show the predominance of *S. elegans* in the central area of the Celtic Sea. Equally evident is the predominance of *S. serratodentata* in the outer area along the edge of the Continental Shelf, and of *S. setosa* in a small area off the mouth of the Bristol Channel and in parts of the English Channel mouth. *S. lyra* was nowhere the dominant species but its occurrence was noticeably limited to the edge of the Continental Shelf (Figs. 11, 12). These distributions are in agreement with Russell's findings. Of the distribution of *S. elegans* in the Celtic Sea, he remarks: 'We do not know how much further this area extends to the south. It may perhaps stretch right across the mouth of the Channel, or it may be reasonably expected that the area changes and lies in fact in the region of the cyclonic circulation known to exist at the mouth of the Channel south of Ireland.' He notes that only *S. serratodentata* occurred in the small area of the Bay of Biscay (centred on 47° 00′ N., 7° 40′ W.) which the *Research* Expedition investigated in 1904 (Russell, 1935*b*). No *S. elegans* were taken beyond the 100 fm. line at the southernmost stations of the *Quentin Roosevelt* cruise of April 1938; *S. serratodentata* only were present (Furnestin, 1939*a*). The distribution of *S. elegans* to the westward in April 1938 and March and April 1939 also indicates that the species does not extend far beyond the western edge of the Continental Shelf. These records show that the distribution of *S. elegans* to the south-west of the British Isles is confined to the Continental Shelf area of mixed oceanic and coastal water (see Russell, 1939*b*, fig. 5, p. 182). It is of interest to compare the above records with the findings of Redfield & Beale (1940) and Clarke, Pierce & Bumpus (1943) in the western Atlantic area of the Gulf of Maine and Georges Bank. In the shallow water (under 100 m.) over Georges Bank there is an anticyclonic eddy carrying a permanent population of *S. elegans* in which no other *Sagitta* species are endemic, although *S. serratodentata*, *S. lyra*, *S. enflata*, *S. maxima* and *Eukrohnia hamata* have been recorded in the area as immigrants from the deeper waters of the Gulf of Maine to the north and the Atlantic to the east. Clarke *et al.* (1943) state: 'The area of relatively homogeneous water overlying the central portion of Georges Bank was found to change in extent from cruise to cruise, but to be sharply delineated from the surrounding stratified water masses, and has been designated as the "Mixed Area".' They also observe that '*S. serratodentata* and *S. enflata*, which were taken chiefly in the September cruise, occurred entirely outside the margin of the Mixed Area.' In the detailed account of the distribution of the *Sagitta* species observed during the present investigation, it is noted that *S. elegans* was most numerous in the southern half of the English Channel mouth and to the west of the Brest Peninsula, particularly in April of each year and to a less marked degree in May–June of 1938 and 1939. In July 1937 and 1938, it was scarce generally. Indications of another area of abundance to the south of Ireland in April 1938 and 1939 rest almost entirely on the evidence from night hauls and cannot therefore be regarded as conclusive, more especially in view of the fact that a small area immediately to the south was devoid of *Sagitta* of any species. The water in the area of the Channel mouth was particularly rich in phosphates in April 1938 (Hickling, 1938) and had a high density of phytoplankton in April 1939 (Mare, 1940). Without further data, it would, however, be premature to correlate the abundance of *S. elegans* with these conditions since the species was not outstandingly numerous at the westernmost stations and in the region off the Bristol Channel mouth where rich phosphate values (April 1938) and dense phytoplankton (April 1939) also occurred.

Gough (1905) gives a comprehensive account of the distribution of *Muggiaea atlantica* over the south-western area in 1904. From the region of Ushant, it spread progressively into the English Channel, the Bristol Channel area, the southern part of the Irish Sea and along the south coast of Ireland. He emphasizes the need for care in drawing conclusions as to water movements from the distribution of an epiplanktonic organism which may be subject to the effects of wind drift in the surface waters and which is capable of rapid asexual reproduction. The hydrological data, however, led Matthews (1909) to agree with his statement that the migrations of *M. atlantica* afforded 'evidence as to the direction of currents during that year'. Russell (1935*b*) also stresses the requirement of caution before including *M. atlantica* in his list of indicators of 'south-western' water. In discussing the occurrence of indicator species at Plymouth in the years 1930–4, he writes: '...it is noticeable that the "south-western" water indicators seem usually to follow the disappearance of "western" water. It appears almost as though we might have here a seasonal phenomenon rather than an indication of water movement, the warm water species increasing when the water is sufficiently warmed.' Evidence from the occurrence of other plankton animals and from hydrological observations is, however, contrary to this interpretation, and he continues: 'There is thus an indication from the plankton observations of a pulse of "western" water entering the Channel, with its maximum about May. This pulse retracts as the pulse of Atlantic water entering the North Sea from the north increases; and this is followed by a pulse of "south-western" water into the Channel.'

In April 1937, *Muggiaea atlantica* was plentiful in the vicinity of Ushant and its distribution extended northwards to the Scilly Isles and westwards from Ushant. It was absent from stations closest to the south coast of Devon and Cornwall (Fig. 13A). Its numbers decreased progessively northwards and westwards from Ushant, pointing to a centre of distribution in that region. It has previously been remarked that a tongue of low salinity water occupied the Channel mouth in April 1937. Comparison of the spread of this fresh water and the distribution of *M. atlantica* leaves little doubt that it carried the *M. atlantica* with it. A single specimen of *M. kochi*[1] was found about 20 miles north of Ushant (St. 5). In this connexion, it should be noted that Russell (1938*b*) records the occurrence in the first half of 1937 of several planktonic species unusual to the Plymouth area. In May and July 1937, no stations were worked in the Ushant area, but *M. atlantica* was present in the northern half of the Channel mouth (including stations nearest the coast), and in the Land's End–Scilly area (Figs. 13B, C). It was considerably more numerous than in April. But this fact and the abundance of the species at Plymouth in the late summer and autumn (Russell, 1938*b*) cannot, in view of Russell's and Gough's cautionary remarks, be taken as evidence of continued transport from the Ushant area. The April invasion of the Channel mouth, however, appears to have been definitely associated with the low salinity inflow from Ushant.

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[1] I am indebted to Mr F. S. Russell for confirming the identification of this specimen.

In April 1938, *M. atlantica* was absent from the southern half of the Channel mouth and the region of Ushant. It only occurred in the coastal waters around the Cornish Peninsula (Fig. 13D). Low salinity water was present in the Ushant area close to the west coast of the Brest Peninsula and round the north-west coast. It was narrowly confined to the coastal region by a warm salt tongue lying farther off the coast. This penetrated from the south-west towards the southern half of the Channel mouth and, judging from the indications of water mixing in the mouth of the Channel, contributed considerably to the higher salinities there. In May–June 1938, all stations were well to the west of Ushant (about 100 miles) and the Channel mouth. *M. atlantica* was present from north of Scilly to the southermost station—some 110 miles west by north of Ushant (Fig. 13E). In July 1938, the distribution of *M. atlantica* was similar to that of April. It was confined to the coastal waters close to the Cornish Peninsula (Fig. 13F). It is probable that this distribution continued for the greater part of the year since it occurred at Plymouth in every month of the year although in rather low numbers (Russell, 1939*a*).

In April 1939, *M. atlantica* occurred in the southern half of the mouth of the Channel. It extended northwards from Ushant to about half-way across the Channel towards Scilly, and eastwards for some little distance along the north coast of the Brest Peninsula (Fig. 13G). The numbers taken were small, but their disposition with a maximum at the Ushant station, indicated both the origin and direction of spread of the species. Salinity conditions in the area were similar to those of April 1937. Low salinity water which was fairly warm in the deeper layers, flowed northwards close to the French coast past Ushant. It spread about half-way across the mouth of the Channel and also along the north coast of the Brest Peninsula. To the west and closely hemming it in to the Ushant coast, was a tongue of slightly more saline water. This extended northwards across the Channel mouth to Scilly and was evidently derived from the salt water beyond the edge of the Continental Shelf. As in April 1937 there seems to be a close correlation between the distribution of *M. atlantica* and the low salinity inflow round the Brest Peninsula. In May–June 1939, *M. atlantica* occurred well out to the south-west in more saline water than in April. It was not found in the northern half of the mouth of the Channel. No stations were worked near the Brest Peninsula. The invasion foreshadowed in April did not take place and it was 'remarkably scarce' at Plymouth that year (Russell, 1940).

The distribution of *M. atlantica* in 1937–9 throws some light on its value as an indicator species and also on the problem of the origins of the water in the western Channel mouth. In particular, the April records together with the hydrological conditions and the yearly observations at Plymouth on other planktonic species appear to relate to the incursion of 'south-western' water, which itself may be derived from water masses from more than one source (Russell, 1939*b*).

In April 1937, an invasion of *M. atlantica* into the Channel mouth was associated with a strong inflow of low salinity water from Ushant. The oceanic *Sagitta serratodentata* was also more extensively distributed in the area than in April of the other two years, although no strongly saline conditions with which it is usually associated were found in the region of the Channel mouth or to the westward. In the first half of the year at Plymouth, several infrequently recorded planktonic organisms were taken (*Discomedusa lobata*, *Pelagia noctiluca*) and also one species new to the area (*Rhincalanus nasutus*) (Russell, 1938*b*).

In April 1938, *Muggiaea atlantica* occurred in the northern half of the Channel mouth only where apparently it had remained 'resident' since the previous autumn when it was numerous (Russell, 1939*a*). Low salinity water lay to the south of Ushant but did not enter the Channel. It was closely confined to the west coast of the Brest Peninsula by an inflow of saline water from the south-west. This spread eastwards into the Channel mouth restraining any northward flow of the fresh water.

In the region of the saline incursion, there was a break in the distribution of *Sagitta serratodentata*, separating a small community of the species round the north-west coast of the Brest Peninsula from the main population farther to the west along the edge of the Continental Shelf. No unusual planktonic species occurred at Plymouth in the first half of the year (Russell, 1939*a*).

In April 1939, fresh water from the Ushant area spread half-way across the Channel mouth carrying with it small numbers of *Muggiaea atlantica*. To the west of this was a more saline intrusion northwards across the mouth of the Channel, similar to that of April 1938. It did not, however, spread so far eastwards into the Channel and was less saline. In the region of its entry from the south it again appeared to split the distribution of *Sagitta serratodentata*. No unusual planktonic species were recorded at Plymouth and *Muggiaea atlantica* was remarkably scarce throughout the year (Russell, 1940).

These records present something of a paradox. There is little doubt that the low salinity inflow of April 1937 carried with it both the *M. atlantica* and certain plankton species not usually taken at Plymouth. These, including *M. atlantica*, are generally considered to be 'oceanic' (Russell, 1938*a*) and would be expected to occur in saline conditions, and not in the low salinities recorded. But in 1938 and 1939, when the April incursion of saline water into the Channel mouth from the south-west was considerable, there was a lack of 'oceanic' species. Their appearance in early 1937, when the area was filled with water of particularly low salinity, suggests that the fresh water on its way to the Channel mouth, had flowed alongside a body of 'oceanic' water containing the *M. atlantica* and the unusual species, and had gathered them into itself in sufficient quantity to transport them across the Channel.

M. atlantica thus transported, was able successfully to maintain a breeding population in an alien locality for a period of at least twelve months (April 1937–8), probably longer, without recruitment or re-seeding from its original stock, and in a considerable salinity range. Without previous records therefore, its presence is unlikely to be of great value in determining the history or origin of the water in which it occurs.

The lack of 'oceanic' species in the saline incursions of April 1938 and 1939, when hydrological conditions would seem to have favoured their occurrence, may be compared with the general lack of plankton in the 'Biscay water' observed off Ushant by Russell in July 1935 (Russell, 1936*a*).

Attempt at more detailed identification of the above records of planktonic species with specific water masses would be little more than groundless speculation. The need, however, for a further extensive series of data in the Channel mouth and to the south—over the edge of the Continental Shelf—is only too apparent. Until this can be achieved, the present records continue to emphasize the acknowledged complexity of the water movements in the Channel mouth and the varied origins of the water masses entering the area.

RESULTS OF THE CRUISES

The Distribution of Mackerel Eggs

1937

12–20 *April* (Fig. 4A).

Spawning was intense in the west and south-west of the area of the cruise. With the exception of Sts. 2 and 22 where less than 100 mackerel eggs per haul were taken, none occurred in the eastern half—in the region of the Channel mouth and to the north of Scilly. The greatest density of eggs was present along the southern line of stations (Sts. 9–15), and their numbers decreased from south-west to north-east of the area. The maximum haul of 32,300 eggs was taken at the westernmost station (St. 14). In the south-west, where spawning was generally intense, there was a concentration (over 18,000 eggs per haul) in the neighbourhood of 49° 30′ N., 8° 40′ W. (Sts. 13–15) and an indication of a second lesser concentration (over 8000 eggs per haul) at 48° 50′ N., 6° 30′ W., some 60 miles east south-east of this and about 60 miles south south-west of Scilly (Sts. 9 and 10).

27–30 *May*[1] (Fig. 4B).

Mackerel eggs were taken at all stations on the cruise, indicating that spawning activity had extended farther to the north-east towards Land's End since April. But a decrease in the intensity of spawning was evident from the fact that the largest haul contained only 8875 eggs (St. 8) compared with 32,300 in April.[2] It was also shown by the smaller numbers of eggs farthest to the south-west (Sts. 5, 6 and 7). The gradation from large numbers of eggs at the westerly stations to few eggs at the easterly stations was again noticeable.

20–26 *July* (Fig. 4C).

The numbers and distribution of mackerel eggs in July revealed that the main spawning to the westward of the Channel mouth had completely finished. No eggs were taken to the west of the Scilly Islands (Sts. 3–13) and only very diminished spawning activity continued inside the Channel mouth. The maximum haul, containing only 135 eggs, was made at the easternmost station off Plymouth (St. 18), and catches at other stations were very considerably less than this.

1938

6–18 *April*[3] (Fig. 5A).

Mackerel eggs were present over nearly the whole area of the Celtic Sea. They were absent from the extreme marginal regions of the area: from the two westernmost Stations (Sts. 18A and SR 89), from the north-eastern area off the Bristol Channel and the St George's Channel (Sts. SR 72, 41 and 43–47), from the northern half of the mouth of the English Channel (Sts. 1, 2, 52–56 and 62), from the area of Ushant and the west coast of the Brest Peninsula (Sts. 5, 6, 58, F 101–F 104, F 118 and F 119), and from the southernmost region (Sts. F 107–F 111). Two centres of very intense spawning activity were evident. The larger outer centre was situated to the south of Ireland between 9 and 10° W. and covered a considerable area from 49° 20′ N. to 50° 10′ N. (Sts. 16, 21, 22, SR 82, SR 85 and SR 86). The smaller inner one was centred on 49° 05′ N., 7° 15′ W., some 60 miles south-south-west of the Scilly Isles (Sts. 10–12). In the outer centre, the maximum haul contained the very large number of 99,333 mackerel eggs (St. SR 86) and catches at other stations in the area ranged from over 6000 to over 19,000. In the inner centre hauls contained between 5000 and 20,000 eggs. The two centres of spawning activity were noticeably localized and the density of mackerel eggs outside them was seldom greater than 400 per haul, except at stations immediately between them (Sts. 13–15, 23 and SR 78) where larger hauls of 1000–3090 eggs occurred. At Station 48, off the mouth of the Bristol Channel, 2020 mackerel eggs were taken.

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[1] On this cruise, plankton was collected by oblique hauls (usual method of working) with a 1 m. stramin net. It has been estimated that the fishing capacity of the 1 m. stramin net is $\frac{1}{4}\times$ that of the 2 m. stramin ring-trawl. Actual numbers of fish eggs, etc. taken on this cruise have therefore been multiplied by four so that comparisons with the results of other cruises may be of the same order.

[2] Station 8 (May 1937) was about 10 miles east of Stations 13 and 15 (April 1937) where 18,570 and 20,500 mackerel eggs were taken.

[3] See also Farran (1939) and Furnestin (1939*a*). A single mackerel egg was taken on 29 March 1938, to the south of Ireland (Furnestin, 1939*a*; St. 12; 50° 22′ N., 9° 55′ W.).

31 *May–5 June* (Fig. 6A).

Mackerel eggs were absent from the westernmost area (Sts. 18–22), but were taken at all other stations on the cruise. Two dense concentrations of eggs were present. The smaller of these lay to the west and north of the Scilly Isles (Sts. 12 and 30; 18,280 and 6075 eggs). The larger was situated to the south of Scilly, outside the mouth of the English Channel (Sts. 3–6; 5320–31,110 eggs). To the west of the two concentrations and between them, mackerel eggs were considerably less numerous. The southern spawning centre of this cruise can be identified with the inner centre of April. The density of eggs was of the same order although slightly larger catches showed an increase of spawning activity since April. Moreover it was situated in the same latitude, having shifted only slightly eastwards from the April position, so that the western station overlapped the position of the eastern station of the April concentration. Mackerel eggs were few or did not occur at all in the area occupied by the large outer spawning centre of April.

19–24 *July* (Fig. 7A).

Spawning was very diminished in intensity compared with that of April and May–June, and no longer occurred in the Celtic Sea to the westward of Scilly. Eggs were present inside the mouth of the Channel as far west as Scilly, and slightly beyond this—to 7° W.—in the area to the north of Scilly. They were absent from the westernmost stations (Sts. 9–12, 21 and 22) and the northernmost station off the Bristol Channel mouth (St. 15). The spawning area had shifted nearly 200 miles eastwards since May–June; the western limit which was then between 9 and 10° W., now lay between 6 and 7° W. The maximum haul of 1600 eggs was taken at the easternmost station (St. 3) and catches were smallest at the westerly stations.

1939

15–18 *March* (Fig. 8).

Small numbers of mackerel eggs occurred in a restricted area at the western edge of the Continental Shelf, about 70 miles south-south-west of Ireland (Sts. 5–8, 16 and 17). The maximum haul contained 118 eggs (St. 8). The area of distribution lay between 10 and 12° W. and did not extend farther north than 51° N. The southern limit was not determined.

16–27 *April* (Fig. 9A).

Spawning had greatly increased both in intensity and extent since the third week in March. Mackerel eggs were distributed throughout the area of the cruises, except in the northern half of the mouth of the English Channel (Sts. 1, 2, 33, 37, 56–58, 61 and 62), at the mouth of the Bristol Channel (Sts. 46 and 47), and at single stations close to Ushant (St. 4), off the southern Irish coast (St. SR 13) and in the central area (St. SR 17). As in April 1938, there were two centres of intense spawning activity to the west and south. The outer centre was situated to the south of Ireland between 9 and 11° W. and extended southwards from 51° 00′ N. to the edge of the Continental Shelf (Sts. 17–19, 22–26 and SR 26–SR 29). The largest hauls, containing between 5950 and 45,025 mackerel eggs, were taken in this centre. In the smaller inner centre, lying some 90–100 miles west of the Brest Peninsula and centred at about 48° 30′ N., 8° 00′ W. (Sts. 9, 11 and 12), spawning was less intense and catches did not exceed 10,000 eggs per haul. The southern boundaries of the two centres were not determined, but it seems probable that they were continuous as one area along the southern edge of the Continental Shelf. Outside the centres, hauls usually contained fewer than 500 eggs. At Station 49, off the mouth of the Bristol Channel, 1250 eggs were taken. It has already been mentioned that a similarly isolated large haul of mackerel eggs (2020) occurred in this area in April 1938.[1]

2–7 *June* (Fig. 10A).

Mackerel eggs were taken at all stations on the cruise and were concentrated in two centres. The northern centre in which the lesser intensity of spawning occurred (maximum haul, 12,075 eggs; St. 22) lay between the south-east coast of Ireland and the north coast of Cornwall (Sts. 13 and 21–26). The southern centre in which spawning was more intense (maximum haul, 28,500 eggs; St. 3) was situated immediately outside the Channel mouth (Sts. 3, 4, 17, 19 and 28). To the westward of the centres, in the region of the outer April centre, few eggs were present. Comparison of the positions of the two centres with those of April shows the extent of the north-eastward movement of spawning. In the northern centre which was almost certainly a continuation of the outer centre of April, a considerable diminution in spawning intensity had taken place. While the southern centre, which from its position was clearly identifiable with the inner April centre, showed, as in 1938, an increase in intensity of spawning since April.

The Distribution of Mackerel Young Stages

1937

12–30 *April* (Fig. 4A).

It was originally stated that no mackerel young stages were taken in April 1937 (Steven & Corbin, 1939). This record requires correction since the identification of eleven young fish, which in the earlier examination could not be determined with certainty, has now been established. A careful comparison of the specimens with the abundant material of later cruises leaves no doubt that they are young mackerel. Ten specimens were taken to the westward of the area of the cruise (Sts. 15 and 29) and a single specimen was taken to the south of the Lizard (St. 35). Elsewhere on the cruise no mackerel young stages were taken.

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[1] St. 48, April 1938, 50° 55′ N., 5° 50′ W.; St. 49, April 1939, 50° 48′ N., 5° 53′ W.

27–30 *May*[1] (Fig. 4B).

Considerable numbers of young stages were caught on this cruise and the main area of their distribution lay to the south-west (Sts. 4–11) where mackerel eggs were generally most numerous. Small numbers were also taken between Land's End and Scilly (Sts. 1 and 15). The largest haul, containing 568 specimens, was recorded to the westward (St. 8, day haul) where the greatest number of eggs was taken.

20–22 *July* (Fig. 4C).

Young stages were very much less numerous than in May and were absent from the westernmost area (Sts. 6–10) where previously they had been numerous. They occurred at the easterly stations where spawning still continued, as well as at a number of stations farther west where no mackerel eggs were recorded. The largest catch (20 specimens, St. 16, day haul) was taken to the south of the Lizard, in the eastern part of the area of distribution of the young stages.

1938

6–18 *April*[2] (Fig. 5A).

The distribution of mackerel young stages was confined to the extreme western and south-western margins of the area, towards the edge of the Continental Shelf and beyond the two main spawning centres (Sts. 16–20, SR 86, SR 88, SR 89, SR 91, SR 92, F 107 and F 109–F 114). They were absent from the central, northern and eastern areas, on the landward side of the spawning centres. The majority of hauls contained fewer than 20 specimens, although 69 were taken in one night haul (St. 17).

31 May–5 *June* (Fig. 6A).

In comparison with the numbers taken in April, mackerel young stages were exceedingly numerous. They were present throughout the area of the cruise except off Land's End (St. 1). Their distribution had shifted very considerably north-east since April and they now occurred in the central area of the Celtic Sea where previously they were not recorded. They reached maximal abundance (over 500 per haul) in a broad belt extending across the area of the cruise from north-west to south-east (Sts. 4, 9, 10, 16 and 24–26), in the centre of which the very large number of 8239 specimens was recorded in a daylight haul (St. 25). Station 4 was the only night haul in the area of maximal

[1] See note 1, p. 91.

[2] See also Farran (1939) and Furnestin (1939*a*).

abundance. To the west and south, and more markedly to the north-east of this area, their numbers progressively decreased. It has been noted that in April the young stages occurred beyond the centres of spawning. This was also evident in May–June.

19–24 *July* (Fig. 7A).

Young stages were present in very small numbers (maximum, 6). They occurred at all stations except the two westernmost (Sts. 10 and 11) and three stations in the middle of the Channel mouth (Sts. 5, 6 and 8). As in July 1937, their distribution extended farther west than that of the eggs and it had shifted very considerably eastwards and slightly northwards since May–June. The western boundary on this cruise lay along about 7° 20′ W., while on the May–June cruise it was to the west of 10° W.

1939

15–18 *March*.

No mackerel young stages were taken on this cruise.

16–27 *April* (Fig. 9A).

The distribution of mackerel young stages was similar to that of April 1938. They were taken at the westerly and southerly stations, mainly beyond the spawning centres, although this tendency was not so marked as in April 1938. They were also slightly more numerous than in April 1938 (maximum 174, St. 22, day haul). The 1939 cruise was about a week later than in 1938, and in consequence the records probably represent a later stage in the distribution of the young mackerel, when more had hatched into the plankton and their spread north-eastwards from the edge of the Continental Shelf was more extended. Single specimens were taken off Ushant (St. 3) and off the mouth of the English Channel (St. 31), and three occurred near the mouth of the Bristol Channel (Sts. 47 and 48), close to the isolated concentration of eggs (St. 49).

2–7 *June* (Fig. 10A).

Young stages were present throughout the area except near the Lizard (St. 1). They were more numerous than in April and were most abundant (maximum 634, St. 7, day haul) in an area lying to the westward of the spawning centres and extending from the south-west of Ireland towards the Brest Peninsula (cf. May–June 1938). Their numbers progressively decreased to the north and east of the area of maximal abundance, and small catches at some of the westernmost stations (Sts. 6, 8, 11 and 12), showed that beyond it they were also becoming fewer. Off the mouth of the Bristol Channel (St. 26, day haul) 59 specimens were taken, close to the position of the small concentration of eggs which occurred there in April.

The Distribution of Pilchard Eggs

1937

12–20 *April* (Fig. 4D).

Spawning occurred in the northern half of the Channel mouth and extended to the west and south-west of Scilly as far as 8° W. The centre of spawning was situated inside the mouth of the Channel, off the south coast of Devon and Cornwall (Sts. 1, 2 and 35; over 10,000 eggs per haul). No eggs were taken in the southern half of the mouth of the Channel (Sts. 3–8, 10, 21 and 22), at the westernmost stations (Sts. 13–16 and 18) and to the north-west of Scilly (Sts. 27–32).

27–30 *May*[1] (Fig. 4E).

Pilchard eggs were taken in the Land's End–Scilly region (Sts. 1–3, 14 and 15); they were absent from the western area (Sts. 4–13). Catches were small (maximum 2800, St. 1) but of the same order of size as those of April from this area. No stations were worked inside the mouth of the Channel where the April concentration was situated.

2–22 *July* (Fig. 4F).

No pilchard eggs were found to the west of Scilly (cf. May 1937) and the spawning area was identical with that of the mackerel (Sts. 1, 2 and 14–18). The largest hauls were taken to the eastward, in the region of the April spawning centre (maximum 10,000 eggs, St. 17).

1938

6–18 *April*[2] (Fig. 5B).

Pilchard eggs were present in a broad area extending from the north coast of Cornwall south-westwards across the entrance to the Channel. The centre of spawning was situated, as in April 1937, in the northern half of the Channel mouth (Sts. 2, 3, 29 and 30), where hauls containing from 7680 to 24,120 were taken. No eggs were present in the western and northern parts of the Celtic Sea nor in the southern half of the mouth of the Channel and off the Brest Peninsula.

31 *May*–5 *June* (Fig. 6B).

The distribution of pilchard eggs on this cruise was similar to that of April, extending from north of the Scilly Isles southwards across the mouth of the Channel (Sts. 2–6, 12 and 30). Only the western limit of distribution was determined, since no stations were worked inside the mouth of the English Channel. They were absent off Land's End (St. 1) and from the western area beyond about 7° 30′ W. The largest hauls were made to the west of Scilly (St. 12; 20,600 eggs) and about 70 miles farther south outside the Channel mouth (St. 5; 25,320 eggs).

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[1] See note 1, p. 91.

[2] See also Furnestin (1939*a*). A single pilchard egg was taken on 24 March 1938, to the south of Ireland (Furnestin, 1939*a*; St. 9; 50° 42′ N., 10° 00′ W.).

19–24 *July* (Fig. 7B).

Pilchard eggs were numerous at the easterly stations. They were absent or scarce to the west of Scilly and towards the southern half of the mouth of the Channel. The main concentrations were situated similarly to those of May–June, off the north coast of Cornwall (Sts. 16 and 17; 950 and 38,600 eggs) and inside the Channel mouth in the northern half (Sts. 1, 2 and 23–26; 2100–22,450 eggs).

1939

15–18 *March.*

No pilchard eggs were taken on this cruise.

16–27 *April* (Fig. 9B).

Pilchard eggs occurred at all stations in the Channel mouth and to the westward as far as 9° W. This was considerably farther west than on previous cruises. They were absent from a small area immediately to the north of Ushant, from the westernmost stations and also the area to the north of the Scilly Isles, except for the occurrence of 27 eggs off the south-east coast of Ireland (St. 42, 1 egg; St. SR 23, 26 eggs). Three spawning centres were present. The largest of these occurred inside the middle of the Channel mouth (Sts. 2, 57, 58 and 61; 13,100–39,075 eggs). The two smaller centres lay farther to the west. One was situated immediately outside the middle of the Channel mouth (Sts. 37 and 55; 23,500 and 92,925 eggs); the other occurred farther to the south, about 90–100 miles west of Ushant (Sts. 10 and 11; 14,500 and 22,975 eggs) in an area immediately adjoining the smaller inner concentration of mackerel eggs.

2–7 *June* (Fig. 10B).

Pilchard eggs were found in the easternmost area of the cruise, near Scilly and the tip of the Cornish Peninsula (Sts. 1–3, 19, 20, 27 and 28); elsewhere to the west and north none was taken. No stations were worked inside the mouth of the Channel. They were very numerous to the south of Land's End and the Lizard, and the exceptionally large haul of 121,950 eggs was taken in this area (St. 1).

The Distribution of Sagitta elegans *Verrill*

1937

12–20 *April* (Fig. 11A).

No *Sagitta* spp. were taken at Stations 1, 25 and 30. *S. elegans* was taken at all other stations and was the dominant species over the whole area with the exception of the two westernmost stations (Sts. 13 and 14) where *S. serratodentata* was more numerous. The numbers per haul show very considerable variation due to diurnal vertical migration, but a general tendency for the species to be less abundant towards the west is noticeable. The largest haul was taken about 20 miles west of Ushant (4610 specimens, St. 7, day haul).

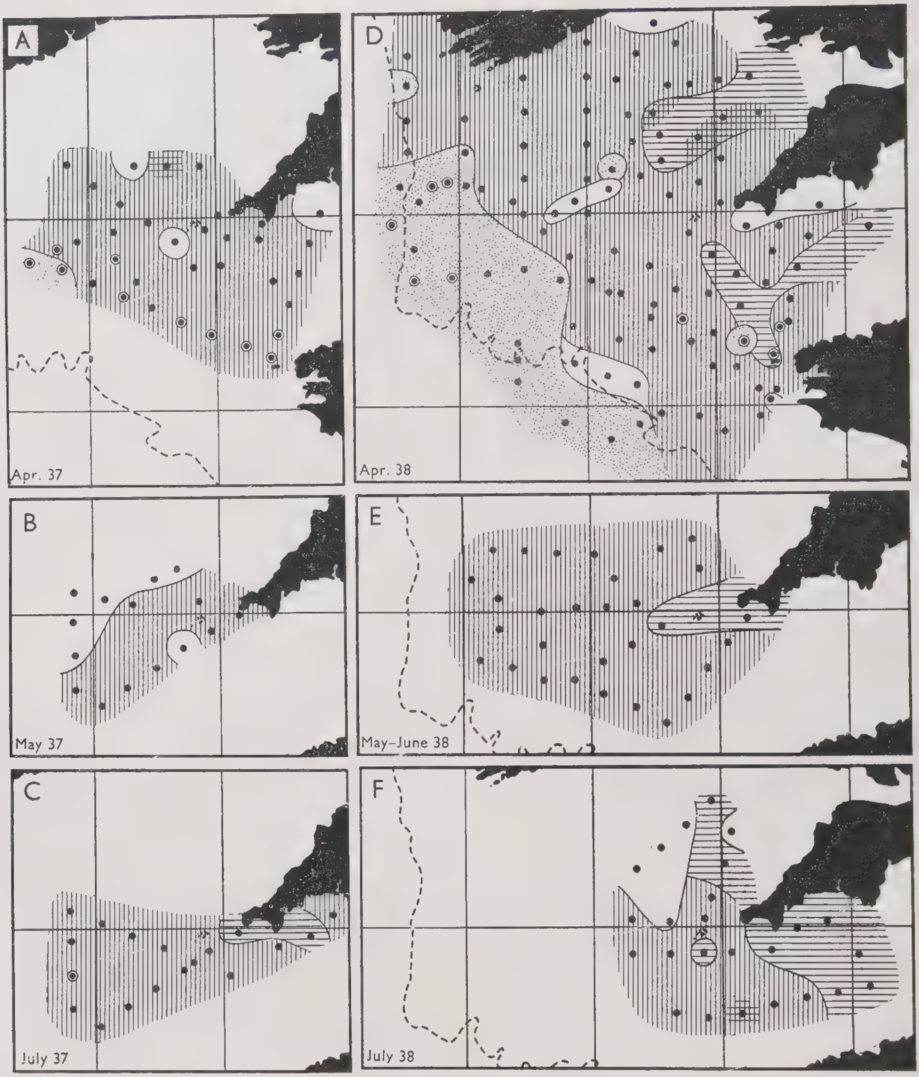
A
Apr. 37
D
Apr. 38
B
May 37
E
May–June 38
C
July 37
F
July 38

Fig. 11. Areas of dominance of *Sagitta elegans* |||, *S. setosa* ≡ and *S. serratodentata* ▒ in the Celtic Sea in 1937 (A, B and C) and 1938 (D, E and F). ⊙ *S. lyra* present.

27–30 *May*[1] (Fig. 11B).

No *Sagitta* spp. were taken at Stations 3, 8–11, 13 and 14. *S. elegans* was recorded at all other stations and was the dominant species throughout the area, although very much less numerous than in April (maximum 300, St. 5, night haul).

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[1] See note 1, p. 91.

20–22 *July* (Fig. 11 C).

The species was taken at all stations on the cruise and was dominant in the whole area with the exception of two separate stations, off Land's End and east of the Lizard, where *S. setosa* predominated (Sts. 1 and 17). Numbers had increased very considerably since May, but were not so great as in April (maxima, 1560 (day) and 2800 (night); Sts. 8 and 13).

1938

7–18 *April*[1] (Fig. 11 D).

No *Sagitta* spp. were taken at Stations 1, 24, 25, 42, 54, SR 78, F 101, F 113–F 115. *S. elegans* was distributed over almost the whole area of the Celtic Sea; it was absent from certain marginal areas (St. 42 in the north; Sts. 18 A, 19 and SR 89 in the west; Sts. 16, F 106–F 110 and F 113–F 115 in the south; Sts. 1, 29, 54 and 59 in the northern half of the Channel mouth) and from one station (St. 36) adjoining the central patch in which no *Sagitta* spp. occurred (Sts. 24, 25 and SR 78). The majority of the large catches of *S. elegans* were taken at night stations (see Table VI), and for this reason the greatest reserve is required in pointing out any particular concentration within the distribution of the species. It seems probable, however, that an area of abundance was present in the vicinity of Ushant (Sts. 4 and 5 (night), 2950 and 3270 specimens; Sts. 6 and 7 (day), 287 and 900 specimens) where both day and night hauls were noticeably larger than those of the surrounding stations. Several large catches were made to the south of Ireland (Sts. 21, 22, 39, SR 73–SR 75 and SR 81–SR 83; 600–5200 specimens) but all occurred at night stations and cannot therefore be considered as representing a true concentration of the species. A large daylight haul was also taken about 30 miles south-west of Valencia (St. SR 93; 1405 specimens). *S. elegans* was the dominant species in the central area of the Celtic Sea from southern Ireland to the approach to Ushant. At the western and south-western stations it was outnumbered by *S. serratodentata*, and in the areas off the entrance to the Bristol and English Channels *S. setosa* was the predominant species.

31 *May*–5 *June* (Fig. 11 E).

S. elegans was taken at all stations. It was the dominant species throughout the area of the cruise except in the region off Land's End past Scilly in which *S. setosa* predominated (Sts. 1 and 11). In the area west of the Channel mouth, very large catches were taken in day and night hauls (Sts. 2, 7, 8, 10, 11, 24 and 25 (day), 600–5820 specimens; Sts. 3 and 4 (night), 7040 and 29,340 specimens). At the westernmost and northernmost stations numbers were generally lower.

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[1] See also Furnestin (1939*a*).

19–24 *July* (Fig. 11 F).

No *Sagitta* spp. were taken at Stations 12, 14 and 16. The area of distribution of *S. elegans* lay to the west of the Channel mouth and extended slightly to the north of the Scilly Isles. A single specimen was taken at the northernmost station (St. 15) and four occurred off Plymouth (Sts. 1 and 26). The species was very much less numerous than in April and in May–June (maxima: St. 9 (day), 500 specimens; St. 21 (night), 1000 specimens).

1939

15–18 *March* (Fig. 12 A).

The species occurred at all stations except the two westernmost (Sts. 8 and 9) and was present in considerable numbers (maxima: St. 1 (day) 700 specimens; St. 20 (dusk) 2850 specimens). It was the dominant species from the area of Scilly westwards to about 10° W. Farther west, *S. serratodentata* was the most numerous species.

16–27 *April* (Fig. 12 B).

No *Sagitta* spp. were taken at Stations 26, 28, 37, 39, 43, 48, 49, SR 13, SR 20, and SR 28. With the exception of the above stations and also Stations 22, SR 21, SR 23 and SR 30, *S. elegans* was distributed over the whole of the Celtic Sea and was taken in particular abundance at the southern half of the mouth of the English Channel in both day and night hauls (Sts. 2–8 and 36; maxima, 6240 (day) and 11,440 (night)). Large catches were also taken in the area to the south of Ireland and west-north-west of Scilly and, although the majority occurred at night stations, two daylight hauls in the area contained considerably greater numbers than at surrounding stations (Sts. 31, 40, 41, 52 and SR 15–SR 19; maxima, 905 (day) and 10,875 (night)). A central patch in which no *Sagitta* spp. occurred (Sts. 26, 28, SR 20 and SR 28) was situated a little to the west of the barren patch of April 1938. *S. elegans* was the dominant species throughout the greater part of the Celtic Sea, including the mouth of the Bristol Channel and the southern half of the mouth of the English Channel. In the northern half of the Channel mouth it was replaced as the dominant species by *S. setosa*, and by *S. serratodentata* in the western area and at some of the southern stations.

2–7 *June* (Fig. 12 C).

No *Sagitta* spp. were taken at Stations 14 and 17. With the exception of these and a single station close to Land's End (St. 28), *S. elegans* occurred throughout the area of the cruise. It was dominant over almost the whole area except at the westernmost station and the southernmost station where *S. serrato-*

dentata was more numerous (Sts. 6 and 12), and in the Land's End–Lizard area where *S. setosa* predominated (Sts. 1 and 28). It was most abundant in the area to the west of the Channel mouth (Sts. 3, 4, 5 and 19; 2100, 950 (day), 1125, 2175 (night)).

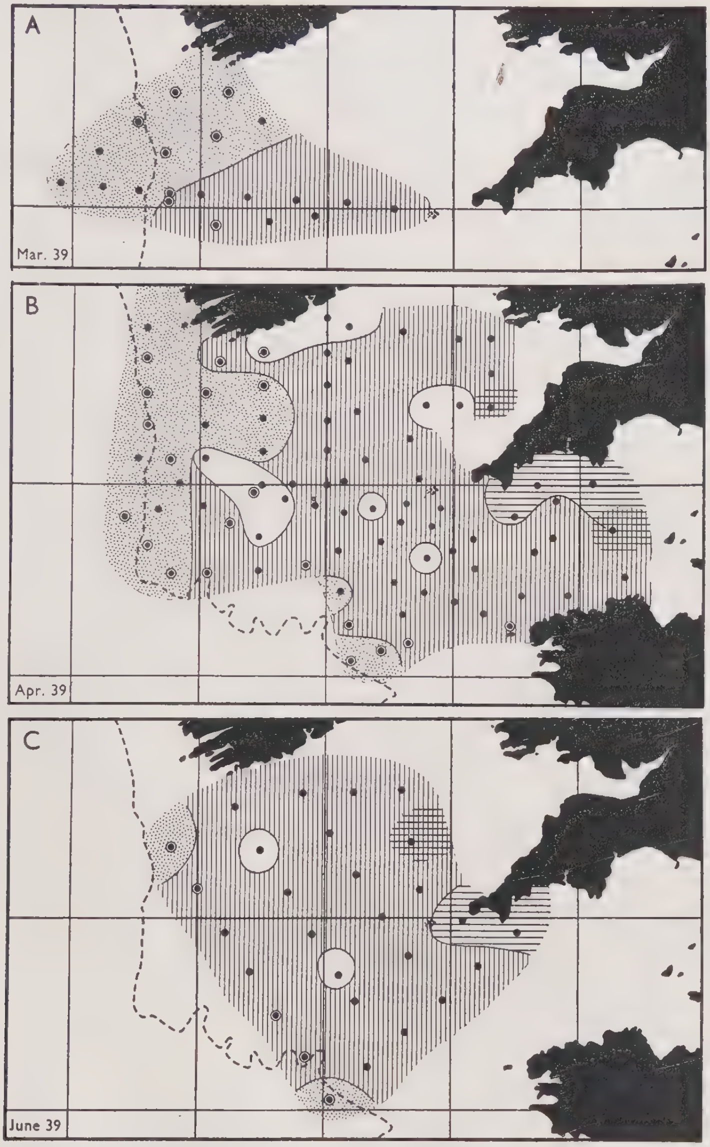

Fig. 12. Areas of dominance of *Sagitta elegans* ||||, *S. setosa* ≡ and *S. serratodentata* ▒ in the Celtic Sea in 1939. ⊙ *S. lyra* present.

The distribution of Sagitta setosa *J. Müller*

1937

12–20 *April* (Fig. 11A).

S. setosa was present from the Channel mouth westwards to 8° W. It was absent off the south coast of Devon and Cornwall (Sts. 1 and 34) and from the area north of Scilly (Sts. 11, 13, 15–17 and 23–25). It was very much less numerous than *S. elegans*. The largest hauls were taken close to Ushant in daylight (Sts. 6 and 7; 166 and 130 specimens); elsewhere numbers were almost all well below 30 per haul. Nowhere was the species dominant.

27–31 *May*[1] (Fig. 11B).

Twenty specimens only were taken, at two stations in the Land's End–Scilly Channel (Sts. 1 and 15).

20–22 *July* (Fig. 11C).

The distribution of *S. setosa* extended westwards from Plymouth to Scilly; west of this it was not taken. It was the dominant species close to Land's End (St. 1) and also to the east of Lizard Head (St. 17). Catches were very much smaller generally than *S. elegans* (maximum 89, St. 1).

1938

6–18 *April*[2] (Fig. 11D).

S. setosa was widespread in the northern and south-eastern areas. It was absent from the western and south-western stations, from a small area in the northern half of the Channel mouth (Sts. 1, 2 and 54–57) and from the region to the south of Ushant (Sts. F 101–F 103, F 118 and F 119). It was considerably less numerous than *S. elegans* (maximum 520) and was particularly scarce (maximum 8) in the area to the south of Ireland and westwards to 10° W. Large catches were taken in day hauls near Ushant (Sts. 6 and 7; 345 and 520 specimens) and in night hauls in the area outside the mouth of the Bristol Channel (maximum, 400 specimens, St. 47). Off the mouth of the Bristol Channel, *S. setosa* was dominant at some stations (Sts. 46, 50A and 51) and present in the same quantity as *S. elegans* at others (Sts. 38, 47, 48 and 50). It was also dominant in a narrow ⊢ shaped area in the mouth of the English Channel (Sts. 3, 6, 29–31 and 62).

31 *May*–5 *June* (Fig. 11 E).

S. setosa occurred in the south-eastern half of the area only. Numbers were very small, generally below 100 per haul, at all stations, with the exception of a large haul of 2300 specimens taken to the west of Scilly in daylight (St. 11). It was the dominant species at this station and off Land's End (St. 1).

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[1] See note 1, p. 91.

[2] See also Farran (1939) and Furnestin (1939*a*).

19–24 *July* (Fig. 11F).

The species was taken in small numbers (maxima: 46 (day), St. 20; 49 (night), St. 18) at the easterly stations, both north of the Cornish Peninsula and in the Channel mouth. It did not occur to the west of Scilly (Sts. 6–14 and 16). It was dominant off the mouth of the Bristol Channel (Sts. 15 and 17) and inside the mouth of the English Channel to the east (Sts. 1–4 and 24–26).

1939

15–18 *March* (Fig. 12A).

One specimen of *S. setosa* was taken about 25 miles south-east of the Fastnet Lighthouse (St. 14).

16–27 *April* (Fig. 12B).

The area of distribution was restricted to the Bristol Channel mouth and the mouth of the English Channel and did not extend westwards of 6° W., with the exception of three specimens taken immediately west of Scilly (Sts. 32 and 52) and a single specimen off the Channel mouth (St. 8). It was also absent from a small area inside the Channel mouth (Sts. 2, 58 and 59). It did not occur as far west as in April 1938 either outside the Channel mouth or to the south of Ireland. In comparison with the large catches of *S. elegans*, it was scarce (maxima: 38 (day), St. 3; 185 (night), St. 62). It was the dominant species in the northern part of the Channel mouth (Sts. 56, 57 and 62). It was not, however, dominant at the entrance to the Bristol Channel as in April 1938, although at one station in this region it occurred in numbers equal to those of *S. elegans* (St. 48; both species, five specimens). At one station immediately south-west of Scilly (St. 32) it also appeared to be dominant; this is, however, probably not significant as the total of *Sagitta* spp. taken was only three specimens—two *setosa* and one *elegans*.

2–7 *June* (Fig. 12C).

The species was taken in small numbers (maximum, 300 (day), St. 3) in the eastern half of the cruise—to the west of the Bristol Channel mouth and the English Channel mouth as far as 8° W. Beyond this it did not occur. It was the dominant species close to Land's End and the Lizard although very few specimens occurred here (Sts. 1 and 28; 8 and 2 specimens).

The Distribution of Sagitta serratodentata *Krohn*

1937

12–20 *April* (Fig. 11A).

The area of distribution of the species was continuous from the southern half of the mouth of the English Channel, along the southern line of stations to the western stations both north and south of Scilly. It was absent from the northern half of the Channel mouth (Sts. 1, 2 and 34–36) and from an area extending south-westwards from Land's End to some 50–60 miles south-west of Scilly (Sts. 17, 19, 23–25, 32 and 33). These two areas were nearly cut off from one another in the vicinity of Land's End by a tongue of *S. serratodentata* (Sts. 20–22) which extended northwards between them across the Channel mouth to within 15 miles of Land's End. The species was dominant at the two westernmost stations (Sts. 13 and 14) and was slightly more numerous generally than *S. setosa* (maxima: 262 (day), St. 8; 285 (night), St. 26). Large catches were made at three day stations in the region of Ushant (Sts. 6–8; 233, 225 and 262 specimens).

27–30 *May*[1] (Fig. 11B).

Very small numbers (maximum 8, St. 6 (night)) were taken in the south-western area only (Sts. 4–7).

20–22 *July* (Fig. 11C).

Catches were also small on this cruise (maximum 58, St. 8 (day)) and the species occurred only to the west of the Scilly Isles (Sts. 3, 6–9 and 11–13).

1938

6–18 *April*[2] (Fig. 11D).

S. serratodentata was widely distributed over the western area of the Celtic Sea from the edge of the Continental Shelf eastwards to about 7° W. It also occurred in the southern half of the mouth of the English Channel and off the Brest Peninsula. It was not taken outside the Bristol Channel (excepting three specimens at St. 47) and the entrance to the St George's Channel, nor in the northern half of the mouth of the English Channel and outside to the south of the Scilly Isles. In the south-eastern area it was absent from several stations (Sts. 8, 9, F 1, F 3, F 101, F 103, F 105 and F 112*b*–F 119) disposed roughly in the shape of a cross (+), the arms of which separated four quarters in which *S. serratodentata* occurred. From a comparison of the distribution in April 1939, it seems probable that the north-south break in distribution was a true discontinuity while the east-west break was not. The numbers per haul of *S. serratodentata* were about equal to those of *S. setosa* except off Ushant (St. 7) where the large catch of 2270 specimens was taken in a day haul. It was the dominant species at this station, over the whole of the south-western marginal area, and at one station in the central area (St. 36), although here only three specimens were taken and no other *Sagitta* spp. were present.

31 *May–5 June* (Fig. 11E).

The species was irregularly distributed over the western half of the cruise and did not occur to the east of 7° W. Very small numbers were taken (maximum 30 (night), St. 7) and it did not predominate in any part of the area.

[1] See note 1, p. 91.

[2] See also Furnestin (1939*a*).

19–24 *July* (Fig. 11F).

One specimen only of *S. serratodentata* was taken outside the Channel mouth (St. 8, day haul).

1939

15–18 *March* (Fig. 12A).

S. serratodentata was present at all except the two easternmost stations (Sts. 8 and 9). The eastern limit of its distribution lay along 8° W. and it was the dominant species to the west of 10° W. Numbers per haul were about equal to those of *S. elegans* (maxima: 850 (day), St. 8; 2310 (night), St. 11).

16–27 *April* (Fig. 12B).

S. serratodentata was present in the western half of the Celtic Sea and along the southern margin. In the western area, its distribution did not extend eastwards of 9° 30′ W.; it was absent from the area south of the entrance to the St George's Channel and off the Bristol Channel. In the east it was absent from the northern half of the mouth of the English Channel and to the west and south of Scilly. Along the southern margin its distribution was discontinuous. There was a break in the neighbourhood of Ushant (6° W.) which separated a small body of *S. serratodentata* in the southern half of the Channel mouth (Sts. 2–5, 36 and 59) from the western population. This distribution shows a close resemblance to that of April 1938 but, owing to the lack of stations, it was unfortunately not possible to determine the southward extent of the break. The species was most numerous towards the edge of the Continental Shelf. It was dominant in the area west of 10° W., and to the south of Ireland, where an eastward extension of its area of dominance reached as far as 9° 30′ W. It was also dominant at the southernmost stations (Sts. 11, 12 and 14). It occurred in greater numbers than *S. setosa* but was not so numerous as *S. elegans* (maxima: 1510 (day), St. 21; 1305 (night), St. SR 33).

2–7 *June* (Fig. 12C).

The area of distribution extended over the western part of the cruise (Sts. 4–12, 15 and 18), from south-west of the Fastnet Light to the region well to the west of the Brest Peninsula. It was entirely absent from the area south of Ireland and outside the Channel mouth. Catches were not so large as in April (maxima: 75 (day), St. 8; 600 (night), St. 5) and it was dominant at the westernmost station (St. 12) and the southernmost station (St. 6) only. It was considerably more numerous than *S. setosa*.

The Distribution of Sagitta lyra *Krohn*

S. lyra occurred in very much smaller numbers than any of the foregoing three species of *Sagitta*. It was not dominant in any of the areas in which it occurred.

1937

12–20 *April* (Fig. 11A).

The species was taken along the southern line of stations from Ushant westwards (Sts. 5–9, 11, 13–15 and 18; maximum 16, St. 7, day haul).

27–30 *May*.

None was taken on this cruise.

20–22 *July* (Fig. 11C).

A single specimen occurred at Station 8 (day haul).

1938

6–18 *April* (Fig. 11D).

The species was present in the neighbourhood of Ushant (Sts. 5–7 and 33) and at some of the westernmost stations (Sts. 16, 17, 18A (maximum 20, dawn haul), 20 and SR 88).

31 *May–5 June, and* 19–24 *July*.

No *S. lyra* were taken on these two cruises.

1939

15–18 *March* (Fig. 12A).

S. lyra occurred in the neighbourhood of 10° W. (Sts. 6, 11–13 and 15–18). It was absent from the westernmost stations (Sts. 7–10) and did not occur very far east of 10° W. It was noticeably more numerous in night hauls (maximum 50, St. 15) than in day hauls (maximum 14, St. 12).

16–27 *April* (Fig. 12B).

The species occurred at a considerable number of stations along the edge of the Continental Shelf from the south-west of Ireland to Ushant. With the exception of a large catch (115 specimens) taken in daylight at the westernmost station (St. 21), no hauls contained more than 18 specimens.

2–7 *June* (Fig. 12C).

The species was present at the southernmost (Sts. 6–8) and westernmost stations (Sts. 11 and 12). The largest haul contained 28 specimens (St. 6, night haul).

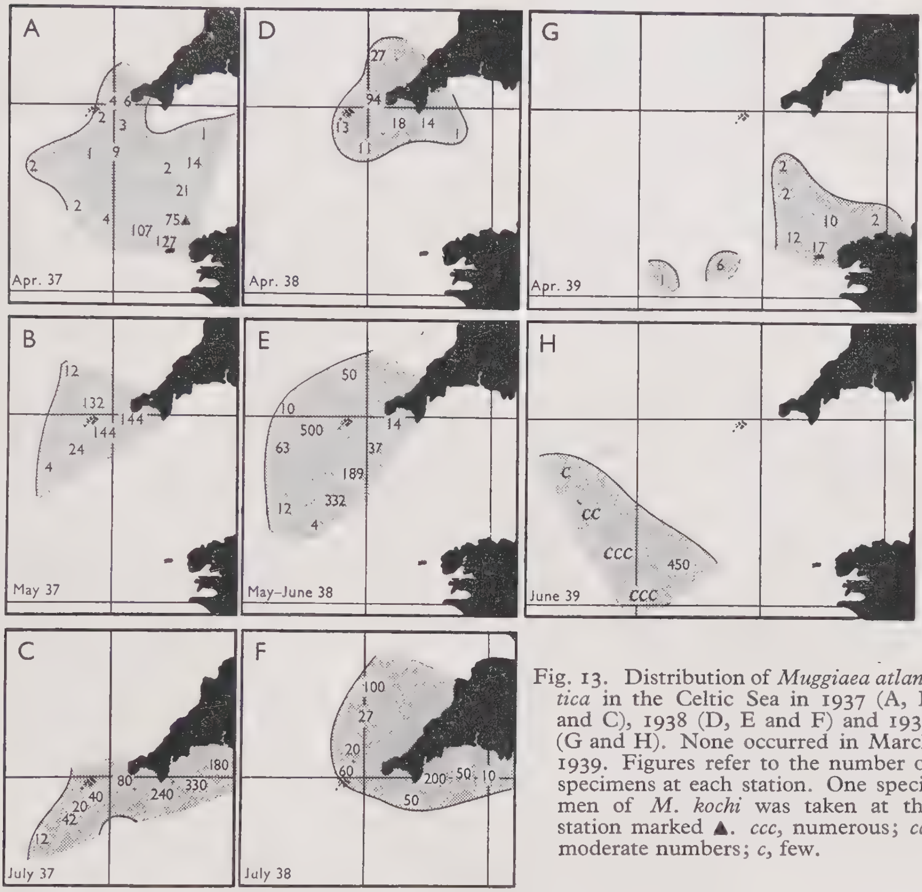
The Distribution of Muggiaea atlantica *Cunningham*

1937

12–20 *April* (Fig. 13A).

M. atlantica occurred in the eastern part of the area of the cruise. It was most numerous in the neighbourhood of Ushant where 75, 127 and 107 specimens were taken (Sts. 5–7, day hauls) and its distribution extended thence across the mouth of the Channel in lessening numbers as far as the

Land's End–Scilly Channel and westwards to 7° W. It was absent off the south coast of Cornwall (Sts. 1, 33 and 34) and from the western and north-western region outside the Channel mouth (Sts. 10–18 and 25–32). A single specimen of *M. kochi* was taken about 20 miles to the north of Ushant (St. 5).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4
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50
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500
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63
37
189
12
332
4
May–June 38
H
c
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June 39
C
180
80
330
240
40
20
42
12
July 37
F
100
27
20
60
200
50
10
50
July 38

Fig. 13. Distribution of *Muggiaea atlantica* in the Celtic Sea in 1937 (A, B and C), 1938 (D, E and F) and 1939 (G and H). None occurred in March 1939. Figures refer to the number of specimens at each station. One specimen of *M. kochi* was taken at the station marked ▲. *ccc*, numerous; *cc*, moderate numbers; *c*, few.

27–30 *May*[1] (Fig. 13B).

The species was taken in the eastern half of the area of the cruise. The western limit of distribution occurred to the west of Scilly at 7° W. No stations were worked to the east of Land's End, inside the mouth of the Channel. It was most numerous in the region of the Land's End–Scilly Channel (Sts. 1 and 2; 144 and 144 specimens; day hauls) and catches here were rather larger than the maximum of April. It was absent from the western stations (Sts. 5–13).

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[1] See note 1, p. 91.

20–22 *July* (Fig. 13C).

The species was taken in the northern half of the Channel mouth and to the west as far as 7° W. No stations were worked in the southern half of the Channel mouth, and the eastern limit of distribution was not determined as the cruise did not extend eastward of 4° W. The largest hauls occurred off the south coast of Devon and Cornwall (Sts. 16, 17 (day hauls) and 18 (dawn haul); 240, 330 and 180 specimens). It was absent from the westernmost stations (Sts. 5–13).

1938

7–18 *April* (Fig. 13D).

M. atlantica was exclusively confined to the coastal waters around the tip of the Cornish Peninsula and the Scilly Islands (Sts. 2, 28, 29, 49 and 53–55). It did not occur in the southern half of the mouth of the Channel nor to the west of Scilly. The largest catch was taken at night between Land's End and Scilly (St. 53; 94 specimens).

31 *May*–5 *June* (Fig. 13E).

M. atlantica was taken in the eastern half of the area of the cruise (Sts. 1–6, 10–12 and 30). Its distribution extended westwards to about 7° 30′ W. and from north of Scilly to the southern margin of the cruise (48° 50′ N.; St. 5). It had spread farther south and slightly farther west since April. The southern and eastern limits of distribution were not determined. It was more numerous than in April, and three large hauls were taken in the area to the south-west of Scilly (Sts. 3, 4 (night hauls) and 11 (day haul); 189, 332 and 500 specimens).

19–24 *July* (Fig. 13F).

The area of distribution was similar to that of April; it was confined to the area around the Cornwall Peninsula (Sts. 1, 16–19 and 24–26) and did not occur in the southern half of the Channel mouth or to the west of Scilly. Numbers were generally slightly less than in May–June (maximum 200, St. 25, day haul).

1939

15–18 *March*.

No *M. atlantica* were taken on this cruise.

16–27 *April* (Fig. 13G).

Very small numbers (maximum 17, St. 4, day haul) were taken in the south-eastern area only—in the southern half of the mouth of the English Channel (Sts. 3–5, 30, 35 and 59) and at two stations some distance to the west of the Brest Peninsula (Sts. 10 and 12).

2–7 *June* (Fig. 13H).

The species was present in the south-western area between 7° W. and 8° 30′ W. (Sts. 5–9). This was considerably farther to the west than on previous cruises. It was absent from the northern and north-western areas and also from the eastern area off the Channel mouth. No stations were worked in the southern half of the Channel mouth, where it occurred in April. Considerably greater numbers were taken than in April (450, St. 5, night haul).

Hydrological Conditions, Temperature and Salinity

No hydrological data were obtained on the cruises of May and July 1937, May–June 1938, and March and June 1939.

12–20 *April.* 1937

Water samples were taken at 5, 25 and 50 m.[1]

Salinity (Fig. 14A). Salinities were vertically homohaline. Water of fairly high salinity (35·31–35·48 $^{0}/_{00}$) lay to the westward of the Channel mouth. It was separated from water of similar salinity inside the Channel—off Plymouth—by a broad tongue of low salinity ($<$ 35·10 $^{0}/_{00}$) which extended northwards from Ushant across the Channel mouth as far as the Lizard. North of the Scilly Isles, salinities were also low (35·09–35·21 $^{0}/_{00}$, total range, all depths; Sts. 32 and 33), but were probably not continuous with the Ushant tongue which appeared to be retained by an eastward extension of slightly more saline water past Scilly to Land's End (35·22–35·30 $^{0}/_{00}$, total range, all depths; Sts. 23 and 24).

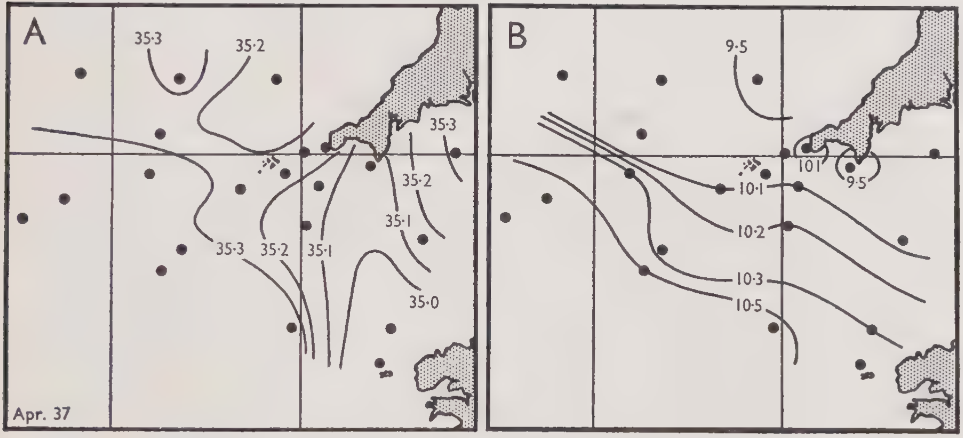

Fig. 14. April 1937; salinities (A) and temperatures (B) at 5 m.

Temperature (Fig. 14B). Temperatures were homothermal at all depths. At Station 23, noticeably high values were recorded, which are however, almost certainly attributable to inshore conditions. The station was less than two miles from the coast of Land's End, in a depth of 20½ fms. (37·5 m.).

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[1] Salinity and temperature data of the April 1937 cruise have been published in the *Bulletin Hydrographique* for the year 1937 (1939).

1938

6–18 April.

Water samples were taken at 0, 5, 25, 50 m. and bottom on the *George Bligh* cruise,[1] at 0, 10, 20, 40, 60, 100, 140, 200 m. and bottom on the *Muirchu* cruise,[2] and at 5, 50, 100 m. and bottom on the *Quentin Roosevelt* cruise.[3]

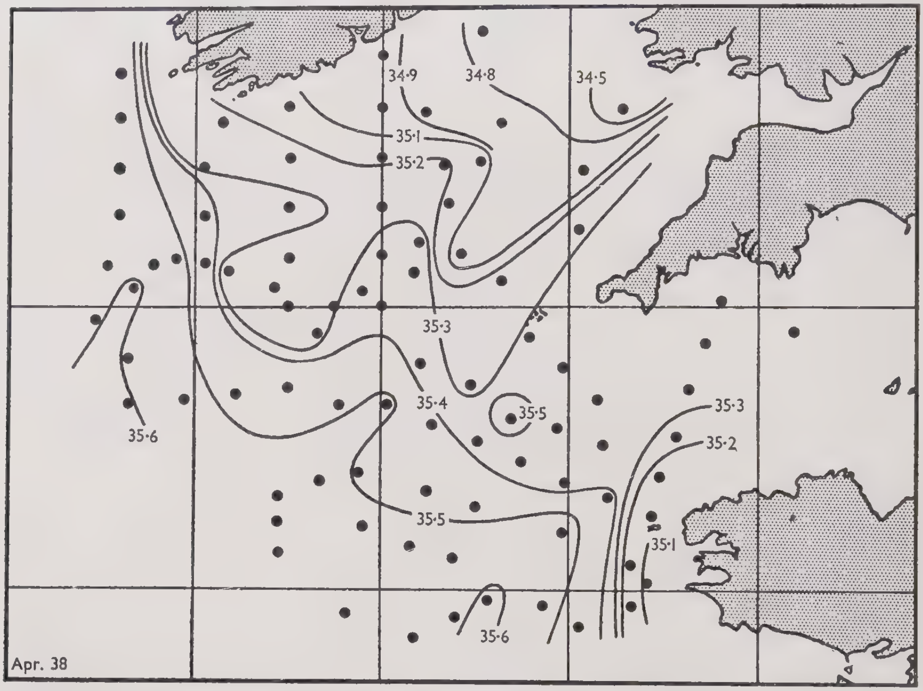

Fig. 15. April 1938; salinities at 5 m. *Muirchu* stations were sampled at 10 m.; there was very little difference between salinities at this depth and at surface.

Salinity (Fig. 15). Conditions were homohaline at all depths. Low salinity water ($<35\cdot20\,^{0}/_{00}$) was present in the south-eastern area—close to the Brest Peninsula, and also in the northern area—from the south coast of Ireland to the mouth of the Bristol Channel. Fairly high salinity water ($35\cdot30$–$35\cdot40\,^{0}/_{00}$) occupied the northern half of the mouth of the Channel and the region to the

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[1] Salinity and temperature data of the *George Bligh* cruise of April 1938 are to be published in the *Bulletin Hydrographique*.

[2] Salinity and temperature data of the *Muirchu* cruise of April 1938 have been published in the *Bulletin Hydrographique* for the years 1938 and 1939 (1944).

[3] For salinity and temperature data, see Furnestin (1939*a*). Data of the first part of the *Quentin Roosevelt* cruise (23 March–5 April 1938) are not included in the above account owing to their slightly earlier date than the *George Bligh* and *Muirchu* observations; data of the second part of the cruise (6–9 April 1938; Sts. F 101–F 119, this paper; 101–119, Furnestin (1939*a*)) are included.

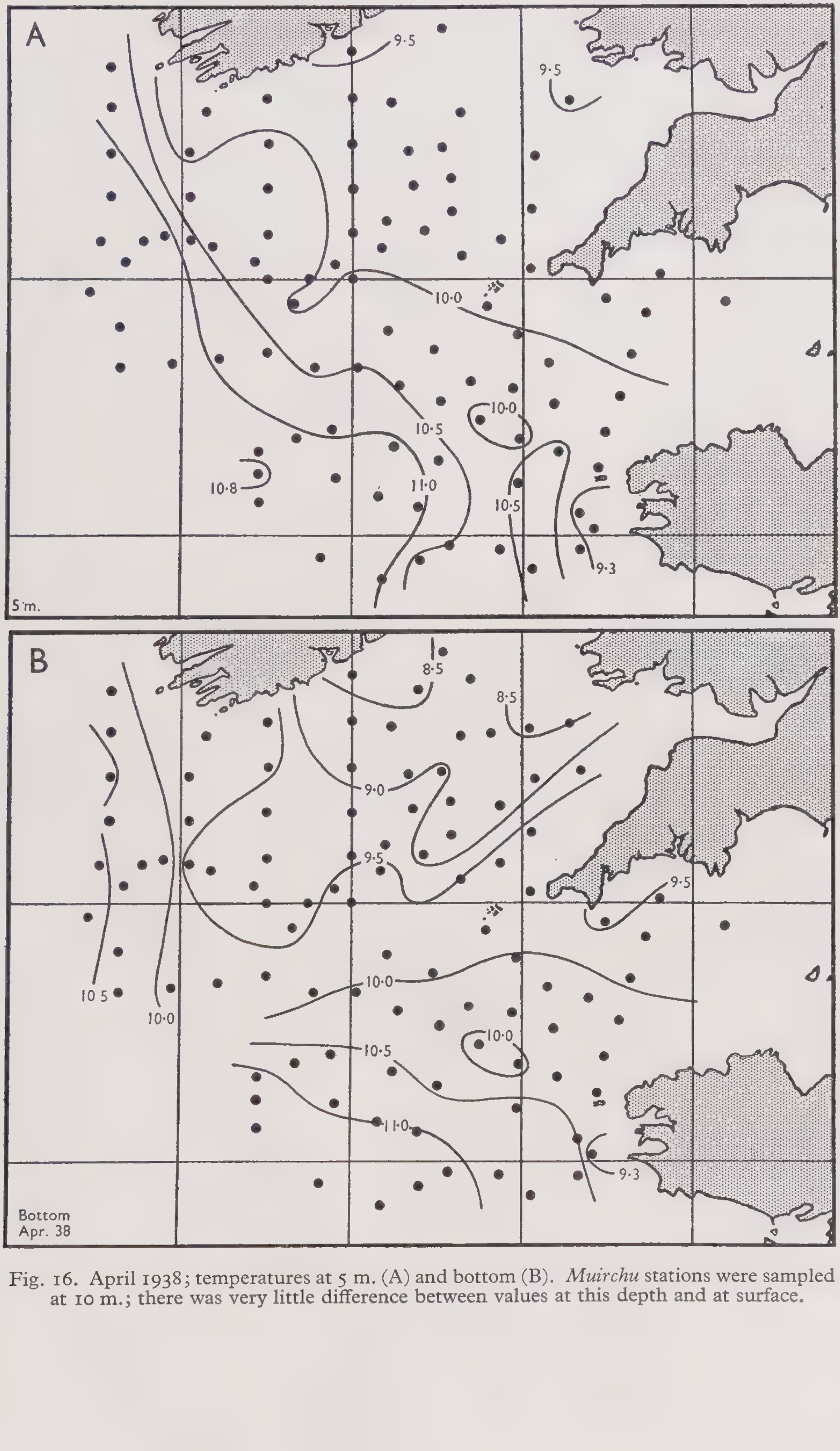
A
9·5
9·5
10·0
10·0
10·5
10·8
11·0
10·5
9·3
5 m.
B
8·5
8·5
9·0
9·5
9·5
10 5
10·0
10·0
10·0
10·5
11·0
9·3
Bottom
Apr. 38

Fig. 16. April 1938; temperatures at 5 m. (A) and bottom (B). *Muirchu* stations were sampled at 10 m.; there was very little difference between values at this depth and at surface.

south of Scilly. High salinities (35·40–35·60‰) prevailed at the western and southern stations. The northern area of low salinity gave rise to two separate tongues of water of salinity below 35·30‰. The first extended southwards along 7° W. to some 35 miles south-west of Scilly (St. 34). The second tongue lay farther to the west and extended in a south-westerly direction between 8 and 10° W., as far south as the latitude of Scilly. The high salinity water along the margin of the Continental Shelf made three incursions into the less saline areas. There was an easterly directed penetration in the area to the south of Ireland. A central one extended northwards along 8° W. to about 50° 30′ N. The close approach of the tips of these two tongues narrowly constricted the root of the western outflow of low salinity water which extended south-westwards between them. The third penetration of saline water, extending northwards towards the mouth of the English Channel, lay off the Brest Peninsula. It confined the low salinity water in the vicinity of Ushant very closely to the French coast. The medium salinities (35·35‰) in the Channel mouth were probably in part derived from this last penetration since small isolated lacunae of higher salinity (35·39–35·51‰) than the surrounding water were found at varying depths (5 m. to bottom) as far east as Station 1 off Plymouth. At two of the southernmost stations (Sts. F 108 and F 109), salinities were slightly lower (35·48 and 35·44‰) at 200 m. than in the upper layers and at stations immediately to the north (35·52–35·59‰).

Temperature (Fig. 16). Temperatures at 5 m. and bottom are shown.

19–24 *July.*

Water samples were taken at 0, 5, 25 and 50 m.[1]

Salinity (Figs. 17A, B). In the surface waters (0 and 5 m.), low salinities were present throughout the area. The maximum value of 35·34‰ was recorded at one station only to the south of Land's End (St. 23, 5 m.), and to the north-west of Scilly, salinities were below 35·10‰. In the deeper layers (25 and 50 m.), slightly more saline water (35·30–35·46‰) occupied the area of the Channel mouth and extended, to the west and north of Scilly, particularly at 50 m. It did not, however, penetrate eastwards into the Channel, where the lower salinities were present at all depths.

Temperature (Figs. 17C, D). Marked thermal stratification occurred over the greater part of the area at 25 m. or just above this depth.

1939

6–18 *April.*

Water samples were taken at 0, 5, 25, 50 m. and bottom on the *George Bligh* cruise and at 0, 10, 20, 40, 60 m. and bottom on the *Muirchu* cruise.[1]

Salinity (Fig. 18). Homohaline conditions prevailed at all depths. Water of very low salinity (< 34·80‰) was present off the mouth of the Bristol Channel and along the south coast of Ireland. With slightly increased salinity (to 35·10‰), it extended south-westwards from the mouth of the Bristol Channel as far as the latitude of the Scilly Isles and to the west of them (St. 31). With a further slight rise of salinity (to 35·30‰), its influence was traceable as a tongue of considerable breadth lying to the west of Scilly and reaching as far south as 49° N. Low salinities (< 35·20‰) were also present in the vicinity of Ushant and occupied the southern half of the mouth of the English Channel. Between these two regions of low salinity, a slightly more saline tongue (35·30–35·38‰) extended northwards along 6° W.—across the mouth of the Channel as far as Scilly. It was evidently derived from the higher salinity water (> 35·50‰) which was present farther to the south at the edge of the Continental Shelf. This saline water occurred in the western and southern areas, and in addition

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[1] Data to be published in the *Bulletin Hydrographique*.

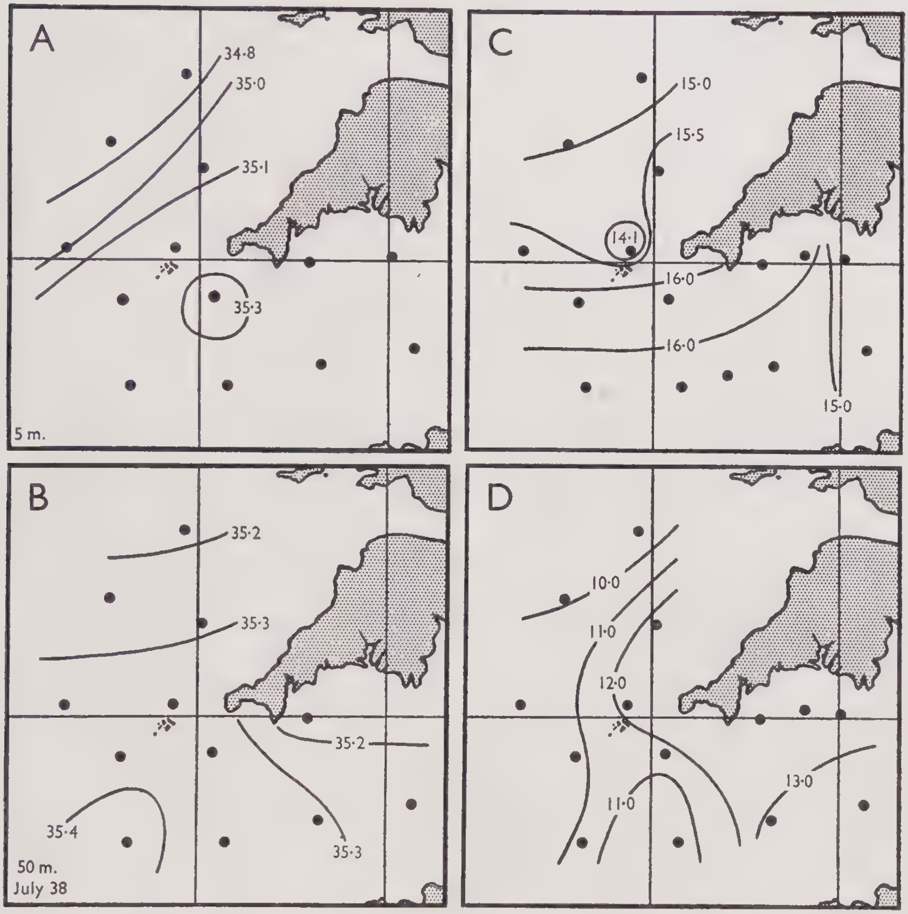

Fig. 17. July 1938; salinities (A and B) and temperatures (C and D) at 5 and 50 m.

to the extension of its influence across the mouth of the English Channel referred to above, there was an easterly directed penetration to the south of Ireland.

Temperature (Fig. 19). Temperatures at 5 m. and bottom are shown.

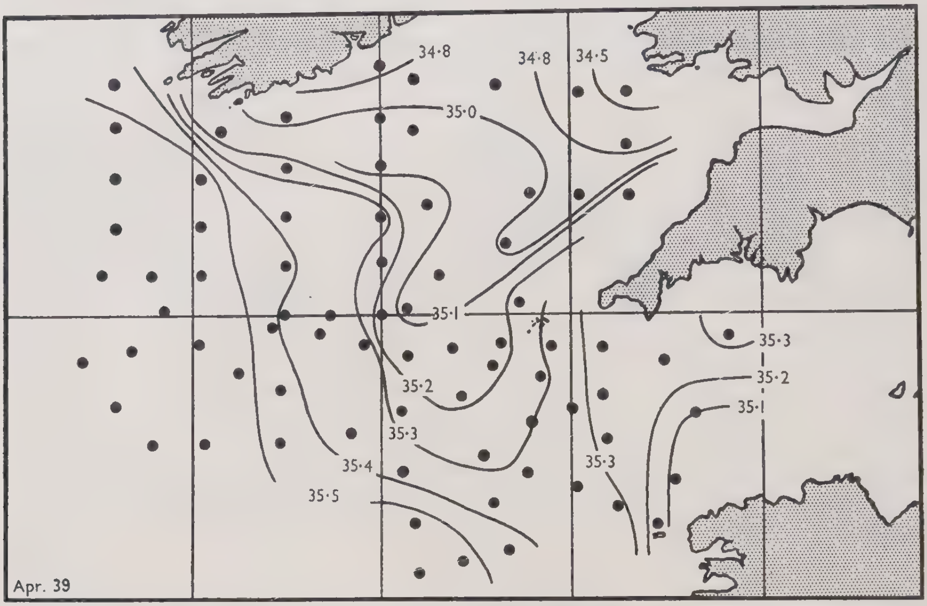

Fig. 18. April 1939; salinities at 5 m. *Muirchu* stations were sampled at 10 m.; there was very little difference between values at this depth and at surface.

2–7 *June.*

Water samples were taken at 5, 25 and 50 m.[1]

Salinity (Fig. 20). Very low salinity water (<34·77 ‰) was present at all depths to the south of the entrance to the St George's Channel (St. 25). In the upper 25 m., its influence extended southwards as a tongue of low salinity (<35·20 ‰) as far as 49° 20′ N., and westwards off the coast of Ireland as far as the Fastnet Light. Below 25 m., it did not reach farther south than 50° 20′ N., nor very far west along the Irish coast. At the western and south-western stations saline water (>35·40 ‰) occurred at all depths, and in the upper 25 m. it extended northwards across the Channel mouth to Scilly (35·59 ‰, 5 m., St. 27, 20 miles north of Scilly) .At 50 m., this northerly flow was checked by slightly fresher water (35·2–35·3 ‰), which extended westwards from the mouth of the Channel, also blocking at this deeper level the southward flow of low salinity water from the St George's Channel region.

Temperature (Fig. 21). Temperatures at 5 and 50 m. are shown.

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[1] Data to be published in the *Bulletin Hydrographique.*

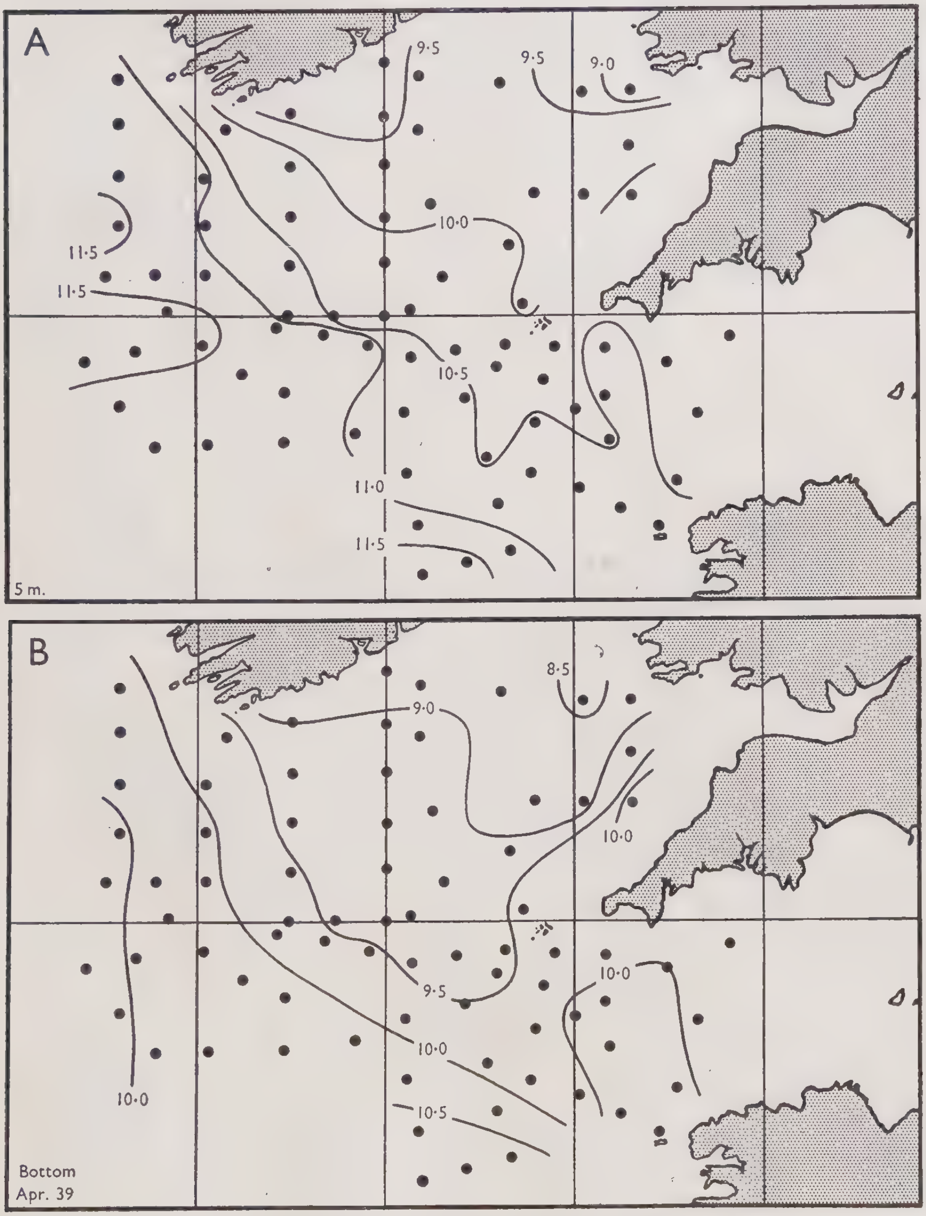
A
9·5
9·5
9·0
10·0
11·5
11·5
10·5
11·0
11·5
5 m.
B
8·5
9·0
10·0
9·5
10·0
10·0
10·5
10·0
Bottom
Apr. 39

Fig. 19. April 1939; temperatures at 5 m. (A) and bottom (B). *Muirchu* stations were sampled at 10 m.; there was very little difference between values at this depth and at surface.

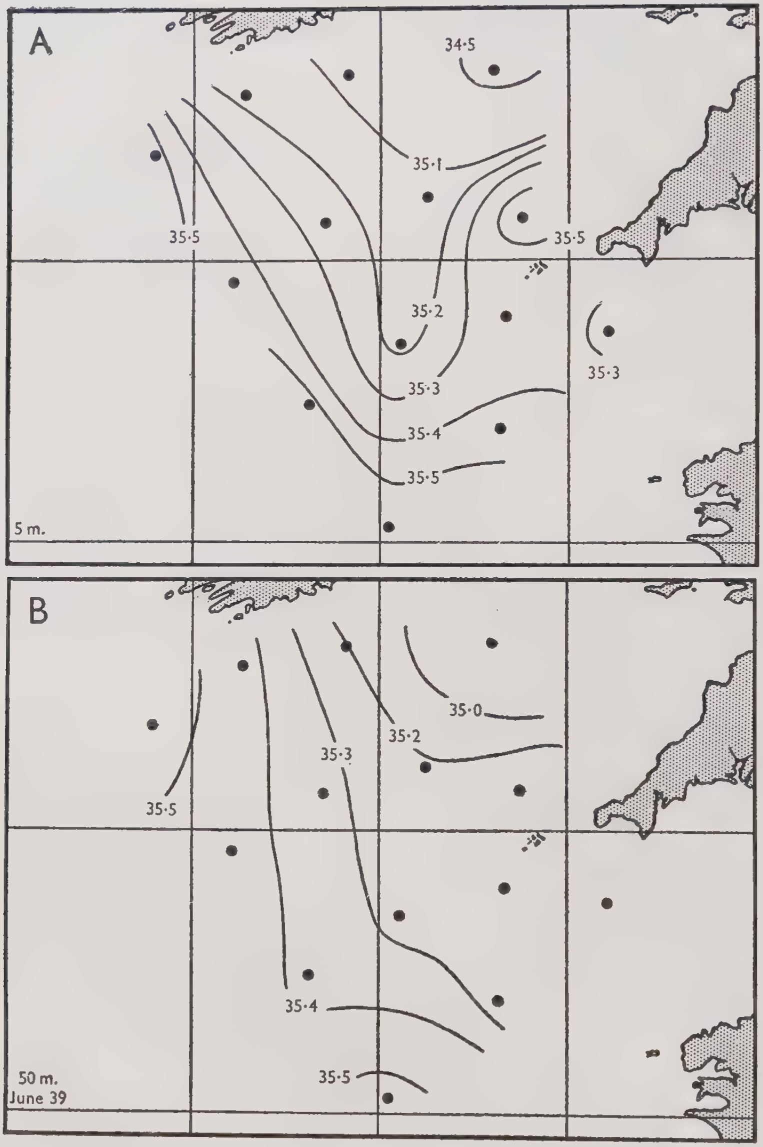
A
34·5
35·1
35·5
35·5
35·2
35·3
35·3
35·4
35·5
5 m.
B
35·0
35·2
35·3
35·5
35·4
35·5
50 m.
June 39

Fig. 20. June 1939; salinities at 5 m. (A) and 50 m. (B).

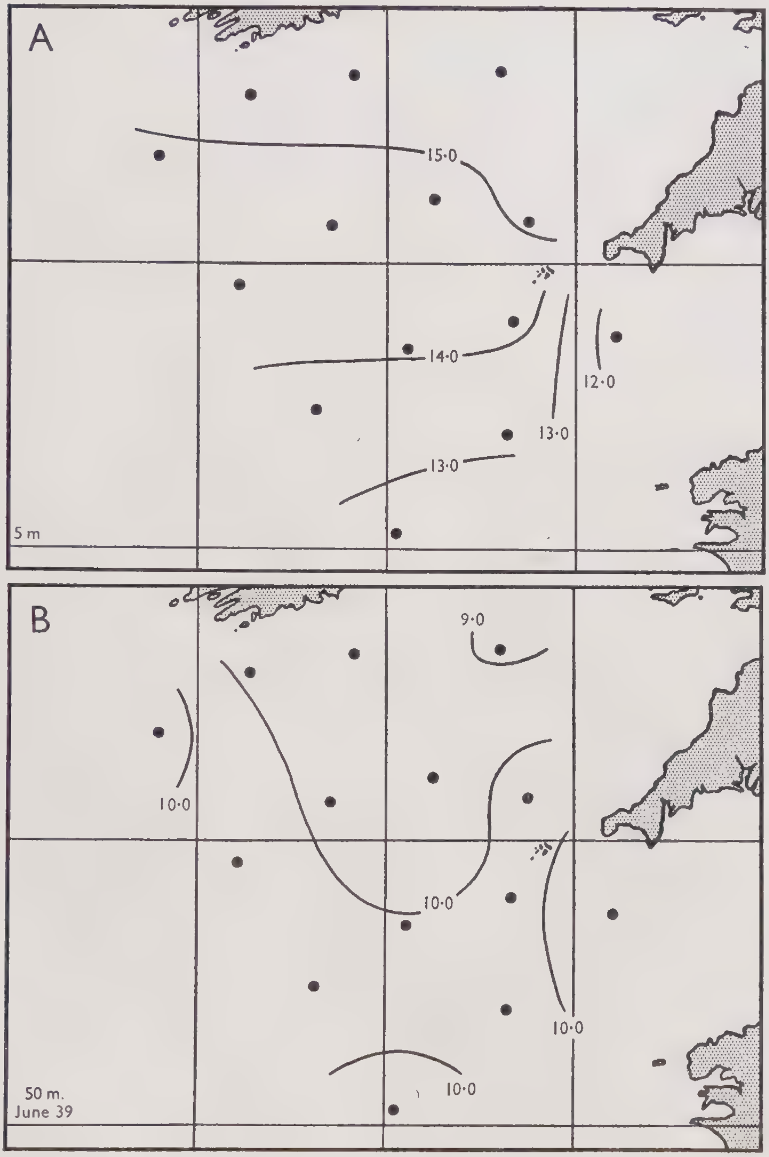
A
15·0
14·0
12·0
13·0
13·0
5 m
B
9·0
10·0
10·0
10·0
10·0
50 m.
June 39

Fig. 21. June 1939; temperatures at 5 m. (A) and 50 m. (B).

SUMMARY

The distributions of mackerel eggs and young stages, pilchard eggs, the siphonophore *Muggiaea atlantica* and the chaetognaths *Sagitta elegans*, *S. setosa*, *S. serratodentata* and *S. lyra* in the Celtic Sea in March 1939, April, May–June 1937, 1938 and 1939 and July 1937 and 1938 are described, together with notes on the hydrological conditions in April 1937, 1938 and 1939, May–June 1939 and July 1938.

Mackerel spawning started in mid-March, rapidly reached a maximum in mid-April, declined gradually through May and June and was very slight at the end of July.

The changes in intensity of spawning are accompanied by a continuous shift eastward and slightly northward of the locus of spawning. In March spawning occurred in a small area at the western edge of the Continental Shelf only. In mid-April it was spread over the greater part of the Celtic Sea, with the main activity concentrated in two centres—to the south of Ireland and to the west of the mouth of the English Channel. By May–June it had shifted farther to the east and occupied the central area of the Celtic Sea. In July there was no spawning to the westward of the Scilly Isles.

The spawning area of the mackerel appears to be confined to the shallow waters over the Continental Shelf.

No mackerel young stages were found in March. Small numbers occurred in April (maximum 174). They were abundant in May–June (maximum 8239), and very scarce in July (maximum 20).

The distribution of young stages closely follows the movement of spawning during the season. In April, they were present to the westward of the spawning centres, along the edge of the Continental Shelf. In May–June, they occurred in greatest abundance to the westward of the spawning centres, but were distributed throughout the Celtic Sea. In July, they did not occur farther to the west than 8° W.

No pilchard eggs were taken in March. Spawning was observed in April, May–June and July, with a maximum in May–June. It occurred in the area of the Channel mouth and westward to about 8° W., and also along the north coast of Cornwall. The main spawning centre was situated in the mouth of the Channel. No spawning took place in the north-western area of the Celtic Sea and it does not appear to extend southwards beyond the edge of the Continental Shelf.

At the western end of the English Channel, spawning lasts from March until December (Russell). It probably occurs throughout the length of the English Channel (Furnestin).

Muggiaea atlantica was not taken in March. It occurred mainly in the mouth of the Channel from April to July. There is evidence that in April 1937

and 1939 it was carried into this area with an inflow of low salinity water from the Ushant area.

Sagitta elegans was the dominant *Sagitta* species throughout the central area of the Celtic Sea on all cruises. Its area of distribution did not appear to extend beyond the Continental Shelf. There was evidence of a centre of abundance in April and May–June to the north-west of Ushant immediately outside the Channel mouth.

Sagitta setosa occurred mainly in the eastern part of the Celtic Sea. It was dominant in parts of the English Channel mouth and off the entrance to the Bristol Channel.

Sagitta serratodentata was distributed over the western and southern areas. It was the dominant species along the edge of the Continental Shelf.

Sagitta lyra occurred along the edge of the Continental Shelf. It was more restricted to this area than *S. serratodentata*.

I am greatly indebted to the late Dr E. J. Allen, C.B.E., F.R.S., who was Director of the Plymouth Laboratory when the mackerel investigation began in 1936, for his advice and warm encouragement to a new worker; and to his successor, the late Dr S. W. Kemp, F.R.S., for generous encouragement and help during the work. My sincere thanks are due to the present Director and staff of the Plymouth Laboratory for their interest, encouragement and practical help throughout the work, particularly to Mr G. A. Steven who was in charge of the investigation. I am much indebted to Mr G. P. Farran of the Fisheries Branch of the Department of Agriculture and Fisheries, Eire, for his kindness in allowing me to examine the complete collections made by the Fishery Cruiser *Muirchu* in April 1938 and 1939 and for his generous permission to use these extensive data. I am indebted to Mr P. H. T. Hartley and to the late Mr P. R. Crimp, for valuable help in the work of some of the cruises. My thanks are also due to Captain W. H. Stewart, lately of the Research Ship *George Bligh* (Ministry of Agriculture and Fisheries), to Mr B. Moore, lately Master of the Lowestoft Steam Drifter *B.T.B.*, to Mr W. H. E. Nichols of Plymouth, lately Master of the Steam Trawler *Elk*, and to the members of the crews of these ships for the great care and interest they showed in the work of the cruises. Part of the preparation of this report was done during tenure of a Leverhulme Research Grant, for which I owe acknowledgement to the Trustees of the Leverhulme Research Fellowships.

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APPENDIX

TABLE VI. NUMBERS OF MACKEREL EGGS, MACKEREL YOUNG STAGES, PILCHARD EGGS AND INDICATOR SPECIES PER ½ HR. OBLIQUE HAUL OF THE 2 M. STRAMIN RING-TRAWL.

* denotes figure obtained by sampling. Nt, night haul. Dn, dawn haul. Dk, dusk haul.

Station number (date in parenthesis)	Station position	Time of haul (G.M.T.)	Mackerel eggs	Mackerel young stages	Pilchard eggs	*Muggiaea atlantica*	*Sagitta elegans*	*Sagitta setosa*	*Sagitta serrato-dentata*	*Sagitta lyra*
				1937						
12–20 April. S.S. *George Bligh*										
1 (12)	50° 01′ N., 4° 21′ W.	17.25–17.55	..	..	12,000*	..	..	..	..	..
2 (12)	49° 42′ N., 4° 32′ W.	20.53–21.27 Nt	6	..	30,000*	1	25	1	..	..
3 (13)	49° 23′ N., 4° 41′ W.	00.13–00.45 Nt	..	..	..	14	2,680*	3	1	..
4 (13)	49° 05′ N., 4° 51′ W.	03.41–04.06 Nt	..	..	..	21	975*	20	29	..
5 (13)	48° 46′ N., 5° 01′ W.	06.54–07.27	..	..	..	75 (1 *M. kochi*)	225*	21	48	4
6 (13)	48° 31′ N., 5° 09′ W.	10.25–10.55	..	..	..	127	800*	166*	233*	4
7 (13)	48° 38′ N., 5° 32′ W.	13.08–13.38	..	..	..	107	4,615*	130*	225*	16
8 (13)	48° 46′ N., 6° 05′ W.	17.03–17.32	440*	..	..	4	471	31	262	1
9 (13)	48° 54′ N., 6° 34′ W.	21.05–21.36 Nt	8,610*	..	17*	2	645*	10*	20*	1
10 (14)	49° 03′ N., 7° 01′ W.	00.25–00.55 Nt	10,080*	..	..	..	1,575*	2	60	..
11 (14)	49° 10′ N., 7° 28′ W.	04.03–04.35 Nt	4,680*	..	80*	..	480*	..	2	3
12 (14)	49° 18′ N., 7° 58′ W.	07.53–08.22	7,012*	..	115*	..	12	1	3	..
13 (14)	49° 27′ N., 8° 26′ W.	11.27–11.56	18,575*	..	..	..	5	..	6	1
14 (14)	49° 32′ N., 8° 58′ W.	15.53–16.23	32,300*	..	..	..	12	1	93	13
15 (14)	49° 40′ N., 8° 30′ W.	19.34–20.04	20,500*	1	..	..	341	..	9	2
16 (14)	49° 44′ N., 8° 11′ W.	22.59–23.29 Nt	1,786*	..	..	..	350*	..	30	..
17 (15)	49° 51′ N., 7° 37′ W.	02.24–02.54 Nt	1,470*	..	675*	..	270*	..	..	..
18 (15)	49° 33′ N., 7° 35′ W.	05.43–06.12 Dn	150*	..	..	..	350*	6	14	3
19 (15)	49° 19′ N., 7° 15′ W.	09.09–09.38	640*	..	5*	2	25	5	..	..
20 (15)	49° 28′ N., 6° 20′ W.	15.52–16.20	2	..	..	1	2,550*	14	11	..
21 (15)	49° 28′ N., 5° 56′ W.	18.09–18.38	..	..	..	9	1,775*	34	127	..
22 (15)	49° 46′ N., 5° 48′ W.	21.17–21.46 Nt	75*	..	485*	3	22	2	1	..
23 (18)	50° 02′ N., 5° 44′ W.	11.54–12.21	..	..	915*	6	275*	1	..	..
24 (18)	49° 51′ N., 6° 10′ W.	15.14–15.42	..	..	1,500*	2	32	1	..	..
25 (18)	49° 45′ N., 6° 38′ W.	18.07–18.36	..	..	760*	..	..	..	..	..
26 (18)	49° 56′ N., 7° 03′ W.	21.18–21.48 Nt	412*	..	630*	..	1,062*	..	285*	..
27 (19)	50° 08′ N., 7° 29′ W.	00.42–01.13 Nt	14	..	..	..	1,127*	..	22	..
28 (19)	50° 19′ N., 7° 55′ W.	03.58–04.27 Dn	9	..	..	..	2,425*	..	4	..
29 (19)	50° 31′ N., 8° 20′ W.	07.04–07.33	577*	10	..	..	15	..	2	..
30 (19)	50° 30′ N., 7° 16′ W.	12.57–13.25	..	..	..	..	..	..	..	..
31 (19)	50° 30′ N., 6° 45′ W.	15.50–16.20	..	..	..	..	3	..	2	..
32 (19)	50° 30′ N., 6° 15′ W.	19.05–19.34 Dk	..	..	..	..	1,870*	..	..	..
33 (20)	50° 01′ N., 5° 58′ W.	01.49–02.19 Nt	..	..	232*	4	138	..	..	..
34 (20)	49° 55′ N., 5° 16′ W.	06.12–06.39	..	..	271	..	57	..	..	..
35 (20)	49° 45′ N., 5° 18′ W.	08.19–08.49	..	1	11,902*	..	48	2	..	..
36 (20)	49° 19′ N., 5° 07′ W.	12.30–13.00	..	..	2	2	342	3	..	..

27–30 May.† Steam drifter *B.T.B.*										
1 (27)	49° 59′ N., 5° 42′ W.	07.48–08.23	36	4	2,800*	144	76	8	..	..
2 (27)	49° 48′ N., 6° 08′ W.	11.20–11.51	60	..	16	144	244	..	..	..
3 (27)	49° 37′ N., 6° 35′ W.	14.20–14.52	1,240	..	336	24	..	..	..	..
4 (27)	49° 25′ N., 7° 00′ W.	18.13–18.44	2,780*	244	..	4	36	..	4	..
5 (27)	49° 13′ N., 7° 27′ W.	19.24–19.56 Nt	276	56	..	..	300*	..	4	..
6 (28)	49° 02′ N., 7° 52′ W.	00.47–01.19 Nt	880	112	..	..	264	..	8	..
7 (28)	49° 12′ N., 8° 17′ W.	03.53–04.23	408	52	..	..	76	..	4	..
8 (28)	49° 33′ N., 8° 17′ W.	07.20–07.52	8,875*	568	..	..	..	..	..	..
9 (28)	49° 54′ N., 8° 18′ W.	10.33–11.12	2,770*	8	..	..	..	..	..	..
10 (28)	50° 12′ N., 8° 18′ W.	13.45–14.17	2,750*	68	..	..	..	..	..	..
11 (28)	50° 08′ N., 7° 48′ W.	16.43–17.15	752	4	..	..	..	..	..	..
12 (28/29)	50° 05′ N., 7° 21′ W.	19.30–04.30 Nt‡	56	..	..	..	88	..	..	..
13 (29)	50° 20′ N., 7° 02′ W.	12.10–12.41	544	..	..	..	..	..	..	..
14 (30)	50° 25′ N., 6° 40′ W.	08.29–09.00	68	..	300*	12	..	..	..	..
15 (30)	50° 06′ N., 6° 19′ W.	11.31–12.02	16	4	200*	132	28	12	..	..
20–22 July. Steam trawler *Elk*										
1 (20)	49° 57′ N., 5° 44′ W.	12.20–12.45	15*	3	2,000*	80*	24	86	..	..
2 (20)	49° 45′ N., 6° 12′ W.	15.15–15.45	35*	4	600*	40*	17	6	..	..
3 (20)	49° 33′ N., 6° 37′ W.	18.10–18.40	..	15	..	42	280*	1	9	..
4 (20)	49° 22′ N., 7° 03′ W.	21.20–21.50 Nt	..	1	..	12	40*	..	..	..
5 (21)	49° 10′ N., 7° 29′ W.	00.22–00.52 Nt	..	1	..	§	§	§	§	§
6 (21)	48° 59′ N., 7° 56′ W.	03.45–04.15 Nt	..	..	..	..	1,700*	..	18	..
7 (21)	49° 09′ N., 8° 22′ W.	06.45–07.15	..	..	..	..	31	..	3	..
8 (21)	49° 30′ N., 8° 22′ W.	10.02–10.32	..	..	..	..	1,566*	..	58	1
9 (21)	49° 51′ N., 8° 23′ W.	13.11–13.41	..	..	..	..	7	..	2	..
10 (21)	50° 10′ N., 8° 23′ W.	16.34–17.04	..	..	..	..	2	..	..	..
11 (21)	50° 02′ N., 7° 54′ W.	19.30–20.00 Dk	..	5	..	..	92	..	2	..
12 (21/22)	49° 55′ N., 7° 25′ W.	22.35–23.05 Nt	..	3	..	..	240*	..	1	..
13 (22)	49° 47′ N., 6° 56′ W.	01.35–02.05 Nt	..	10	..	..	2,800*	..	1	..
14 (22)	49° 38′ N., 6° 28′ W.	06.02–06.32	1	2	350*	20	10	1	..	..
15 (22)	49° 30′ N., 5° 54′ W.	10.00–10.30	5	2	18	..	73	27	..	..
16 (22)	49° 48′ N., 5° 07′ W.	13.08–13.38	25*	20	400*	240*	180*	20*	..	..
17 (22)	49° 54′ N., 4° 37′ W.	16.02–16.32	35*	1	10,000*	330*	6	38	..	..
18 (22)	50° 07′ N., 4° 15′ W.	19.10–19.35	135*	11	1,700*	180*	18	4	..	..

† See note 1, p. 91.

‡ Metre-net attached to foot rope of mackerel drift-nets which were fishing during the night.

§ Haul lost owing to enemy action before these organisms were counted.

TABLE VI (*cont.*)

Station number (date in parenthesis)	Station position	Time of haul (G.M.T.)	Mackerel eggs	Mackerel young stages	Pilchard eggs	*Muggiaea atlantica*	*Sagitta elegans*	*Sagitta setosa*	*Sagitta serrato-dentata*	*Sagitta lyra*
1938										
7–18 April. S.S. *George Bligh*										
1 (7)	50° 02′ N., 4° 22′ W.	13.16–13.53	..	..	1,100*	..	..	..	..	..
2 (7)	49° 43′ N., 4° 32′ W.	17.18–17.48	..	..	24,120*	1	1	3	..	..
3 (7)	49° 24′ N., 4° 42′ W.	20.10–20.40	135*	..	7,680*	..	31	36	..	..
4 (7/8)	49° 05′ N., 4° 50′ W.	23.52–00.22 Nt	42	..	..	..	2,950*	350*	33	..
5 (8)	48° 48′ N., 5° 00′ W.	04.19–04.50 Nt	..	..	..	..	3,275*	72	62	3
6 (8)	48° 31′ N., 5° 06′ W.	09.20–09.50	..	..	..	..	287	345	67	2
7 (8)	48° 39′ N., 5° 34′ W.	12.39–13.09	6	..	..	..	900*	525*	2,270*	3
8 (8)	48° 45′ N., 6° 02′ W.	16.00–16.30	230*	..	755*	..	8	6	..	..
9 (8)	48° 53′ N., 6° 30′ W.	19.09–19.39	155*	..	20*	..	230*	..	..	..
10 (8)	49° 02′ N., 6° 58′ W.	22.27–23.00 Nt	12,500*	..	1,940*	..	480*	5	14	..
11 (9)	49° 10′ N., 7° 27′ W.	01.54–02.24 Nt	20,310*	..	465*	..	105*	..	7	..
12 (9)	49° 18′ N., 7° 57′ W.	05.11–05.41 Dn	5,920*	..	30*	..	4	..	2	..
13 (9)	49° 18′ N., 8° 27′ W.	08.38–09.08	1,717*	..	..	..	27	..	46	..
14 (9)	49° 25′ N., 9° 00′ W.	12.02–12.33	3,650*	..	..	..	2	1	20	..
15 (9)	49° 22′ N., 9° 34′ W.	15.22–15.52	3,090*	..	..	..	1	..	21	..
16 (9)	49° 20′ N., 10° 07′ W.	18.40–19.10	6,580*	1	..	..	..	..	6	2
17 (9)	49° 18′ N., 10° 42′ W.	22.06–22.36 Nt	125	69	..	..	325*	..	500*	1
18 (10)	49° 37′ N., 10° 43′ W.	01.35–02.06 Nt	32	21	..	..	27	..	51	..
18*a* (10)	49° 53′ N., 11° 03′ W.	05.21–06.16 Dn	..	4	..	..	..	..	63	20
19 (10)	50° 07′ N., 10° 39′ W.	13.27–13.57	79	3	..	..	..	..	9	..
20 (10)	50° 18′ N., 10° 11′ W.	18.11–18.41	156	7	..	..	13	..	74	2
21 (10)	50° 14′ N., 9° 39′ W.	22.56–23.26 Nt	12,650*	..	..	..	925*	..	26	..
22 (11)	50° 07′ N., 9° 10′ W.	03.30–04.00 Nt	19,755*	..	..	..	3,150*	..	125*	..
23 (11)	49° 48′ N., 8° 41′ W.	07.33–08.03	1,000*	..	..	..	9	2	1	..
24 (11)	50° 06′ N., 8° 11′ W.	11.21–11.51	435	..	..	..	..	..	..	..
25 (11)	50° 13′ N., 7° 38′ W.	14.51–15.21	203	..	..	..	..	..	..	..
26 (11)	50° 21′ N., 7° 08′ W.	18.18–18.52	12	..	..	..	420*	100*	1	..
27 (11)	50° 10′ N., 6° 42′ W.	22.27–22.58 Nt	100*	..	..	..	62	1	..	..
28 (12)	49° 46′ N., 6° 24′ W.	04.09–04.39 Nt	30*	..	300*	13	24	10	..	..
29 (12)	49° 33′ N., 6° 03′ W.	07.31–08.02	10*	..	10,030*	11	..	2	..	..
30 (12)	49° 20′ N., 5° 40′ W.	11.02–11.32	25*	..	16,200*	..	5	40	..	..
31 (12)	49° 01′ N., 5° 36′ W.	14.23–14.53	41	..	30	..	7	31	..	..
32 (12)	49° 09′ N., 6° 06′ W.	17.42–18.12	123	..	332	..	4	1	..	..
33 (12)	49° 11′ N., 6° 37′ W.	21.01–21.31 Nt	316	..	6	..	1,675*	150*	..	1
34 (13)	49° 26′ N., 7° 01′ W.	00.26–00.56 Nt	483	..	97	..	240*	..	..	..
35 (13)	49° 35′ N., 7° 33′ W.	03.48–04.18 Nt	233	..	..	..	70*	..	2	..
36 (13)	50° 25′ N., 7° 35′ W.	10.52–11.22	315	..	..	..	..	..	3	..
37 (13)	50° 41′ N., 7° 16′ W.	14.58–15.36	36	..	..	..	80	52	7	..
38 (13)	50° 58′ N., 6° 57′ W.	18.36–19.06	26	..	..	..	92	93	2	..
39 (13)	50° 57′ N., 7° 20′ W.	21.50–22.20 Nt	14	..	..	..	2,360*	154	8	..

40 (14)	50° 18′ N., 7° 30′ W.	01.16–01.46 Nt	60*	..	..	..	161	35	9	..
41 (14)	51° 33′ N., 7° 11′ W.	04.39–05.09 Dn	..	..	..	..	62	14	1	..
42 (14)	51° 50′ N., 6° 55′ W.	08.07–08.37	30*	..	..	..	..	..	..	..
43 (14)	51° 38′ N., 6° 36′ W.	11.22–11.54	..	..	..	..	52	10	..	..
44 (14)	51° 14′ N., 6° 24′ W.	14.56–15.26	..	..	..	..	71	22	..	..
44*a* (14)	51° 15′ N., 6° 18′ W.	17.42–17.55	..	..	..	..	88	24	..	..
45 (14)	51° 17′ N., 5° 55′ W.	20.12–20.42 Nt	..	..	..	..	360*	300*	..	..
46 (14)	51° 19′ N., 5° 25′ W.	23.29–00.00 Nt	..	..	..	..	31	36	..	..
47 (15)	50° 58′ N., 5° 19′ W.	02.40–03.10 Nt	..	..	..	..	400*	400*	3	..
48 (15)	50° 55′ N., 5° 50′ W.	06.04–06.34 Dn	2,020*	..	..	..	118	112	..	..
49 (15)	50° 31′ N., 5° 52′ W.	10.00–10.30	10*	..	80*	27	76	62	..	..
50 (15)	50° 43′ N., 6° 15′ W.	13.18–13.48	15	..	..	..	1	1	..	..
50*a* (15)	50° 45′ N., 6° 50′ W.	16.33–17.03	3	..	..	..	72	92	..	..
51 (15)	50° 30′ N., 6° 49′ W.	19.56–20.26 Dk	107	..	..	..	34	55	..	..
52 (16)	50° 17′ N., 6° 14′ W.	00.33–01.03 Nt	..	..	960*	..	200*	150*	1	..
53 (16)	50° 04′ N., 5° 54′ W.	03.54–04.24 Nt	..	..	17	94	38	7	..	..
54 (16)	49° 50′ N., 5° 30′ W.	07.31–08.02	..	..	6	18	..	..	..	..
55 (16)	49° 50′ N., 5° 00′ W.	11.58–12.28	..	..	3,360*	14	31	..	..	..
56 (16)	49° 34′ N., 5° 06′ W.	15.43–16.14	..	..	13,000*	..	13	..	..	..
57 (16)†	49° 15′ N., 5° 12′ W.	18.25–18.55	..	..	..	..	68	..	..	..
58 (17)†	48° 51′ N., 4° 51′ W.	01.27–01.57 Nt	..	..	..	..	248	..	..	..
59 (18)†	49° 49′ N., 3° 37′ W.	12.22–12.52	..	..	328*	..	12	..	..	..
7–12 April. Fishery cruiser *Muirchu*										
SR 2872 (7)	51° 40′ N., 8° 00′ W.	18.07–18.40	..	..	..	..	164	6	4	..
SR 2873 (7)	51° 20′ N., 8° 00′ W.	21.20–21.55 Nt	50*	..	..	..	650*	9*	11*	..
SR 2874 (8)	51° 00′ N., 8° 00′ W.	00.25–01.00 Nt	25	..	..	..	1,285*	40	24	..
SR 2875 (8)	50° 40′ N., 8° 00′ W.	03.39–04.15 Nt	81	..	..	..	5,200*	8*	136*	..
SR 2876 (8)	50° 20′ N., 8° 00′ W.	06.40–07.15	461	..	..	..	22	4	1	..
SR 2877 (8)	50° 00′ N., 8° 00′ W.	09.30–10.05	138	..	..	..	8	2	5	..
SR 2878 (8)	50° 00′ N., 8° 30′ W.	12.22–12.55	1,220*	..	..	..	..	..	..	..
SR 2879 (8)	50° 00′ N., 9° 00′ W.	15.10–16.00	15,380*	..	..	..	1	..	..	..
SR 2880 (8)	50° 20′ N., 9° 00′ W.	18.35–19.09	13,350*	..	..	..	4	..	1	..
SR 2881 (8)	50° 40′ N., 9° 00′ W.	21.54–22.28 Nt	8,130*	..	..	..	2,174*	6*	69*	..
SR 2882 (9)	51° 00′ N., 9° 00′ W.	01.05–01.39 Nt	8,380*	..	..	..	1,037*	4	53	..
SR 2883 (9)	51° 20′ N., 9° 00′ W.	04.42–05.16 Dn	487*	..	..	..	1,670*	8	12	..
SR 2884 (9)	51° 14′ N., 9° 43′ W.	10.58–11.31	1,850*	..	..	..	24	1	3	2
SR 2885 (11)	50° 56′ N., 9° 55′ W.	11.00–11.34	6,180*	..	..	..	285	1	35	..
SR 2886 (11)	50° 36′ N., 9° 55′ W.	14.07–14.40	99,333*	23	..	..	21	1	114	..
SR 2887 (11)	50° 16′ N., 9° 55′ W.	17.18–17.51	2,730*	..	..	..	3	..	4	..
SR 2888 (11)	50° 16′ N., 10° 26′ W.	20.26–20.49 Dk	126	9	..	..	17	..	40	1
SR 2889 (11/12)	50° 16′ N., 10° 57′ W.	23.48–00.22 Nt	..	3	..	..	..	..	59	..
SR 2890 (12)	50° 36′ N., 10° 48′ W.	03.11–03.45 Nt	780*	..	..	..	33	..	23	..
SR 2891 (12)	50° 56′ N., 10° 48′ W.	06.39–07.12	840*	6	..	..	5	..	1	..
SR 2892 (12)	51° 16′ N., 10° 48′ W.	09.46–10.20	321	17	..	..	4*	..	28*	..
SR 2893 (12)	51° 33′ N., 10° 48′ W.	12.53–13.27	136	..	..	..	1,405*	..	181	..

† Owing to bad weather, a 1 m. stramin net was used; it was fished over the side while the ship drifted. Counts have therefore been multiplied by 4.

TABLE VI (*cont.*)

Station number (date in parenthesis)	Station position	Time of haul (G.M.T.)	Mackerel eggs	Mackerel young stages	Pilchard eggs	*Muggiaea atlantica*	*Sagitta elegans*	*Sagitta setosa*	*Sagitta serrato-dentata*	*Sagitta lyra*
				1938						
31 May–5 June.	Steam trawler *Elk*									
1 (31)	49° 56′ N., 5° 33′ W.	15.55–16.25	2(?)	..	..	14	7	85	..	..
2 (31)	49° 40′ N., 5° 51′ W.	19.44–20.14	870*	1	2,030*	37	1,000*	90*	..	..
3 (31)	49° 23′ N., 6° 11′ W.	23.03–23.33 Nt	5,320*	41	440*	189	7,040*	170*	..	..
4 (1)	49° 06′ N., 6° 30′ W.	02.40–03.10 Nt	31,110*	898	600*	332	29,340*	30*	..	..
5 (1)	48° 50′ N., 6° 49′ W.	04.48–05.18 Dn	12,200*	307	25,320*	4	55	5	..	..
6 (1)	49° 00′ N., 7° 18′ W.	09.08–09.38	8,010*	141	20*	12	4	..	..	..
7 (1)	49° 08′ N., 7° 48′ W.	16.28–16.58	157	128	..	..	5,820*	30*	30*	..
8 (2)	49° 17′ N., 8° 15′ W.	04.06–04.36 Dn	700*	120	..	..	1,140*	10*	..	..
9 (2)	49° 28′ N., 7° 48′ W.	07.37–08.07	3,120*	1,219	..	..	390*	..	..	..
10 (2)	49° 39′ N., 7° 20′ W.	10.46–11.16	921	672	..	63	1,200*	3	1	..
11 (2)	49° 50′ N., 6° 53′ W.	13.31–14.01	136	369	..	500*	600*	2,300*	..	..
12 (2)	50° 04′ N., 7° 16′ W.	16.55–17.25	18,280*	56	20,600*	10	9	4	1	..
13 (2)	50° 19′ N., 7° 37′ W.	19.54–20.24	748	20	..	..	70	..	2	..
14 (2)	50° 33′ N., 7° 59′ W.	23.09–23.39 Nt	542	63	..	..	120	..	8	..
15 (3)	50° 34′ N., 8° 31′ W.	02.40–03.20 Nt	3,430*	214	..	..	260*	..	..	..
16 (3)	50° 35′ N., 9° 03′ W.	06.00–06.30	2,570*	659	..	..	10	..	..	..
17 (3)	50° 36′ N., 9° 33′ W.	09.16–09.46	72	21	..	..	81	..	..	..
18 (3)	50° 19′ N., 9° 52′ W.	12.17–12.47	..	193	..	..	196	..	1	..
19 (3)	50° 07′ N., 9° 28′ W.	15.30–16.00	2(?)	245	..	..	290*	..	2	..
20 (3)	49° 48′ N., 9° 28′ W.	18.50–19.20	..	277	..	..	78	..	..	..
21 (4)	49° 30′ N., 9° 44′ W.	00.00–00.30 Nt	..	94	..	..	33	..	10	..
22 (4)	49° 24′ N., 9° 15′ W.	04.12–04.42 Dn	..	173	..	..	28	..	..	..
23 (4)	49° 17′ N., 8° 45′ W.	07.21–07.51	219	352	..	..	..	..	4	..
24 (4)	49° 39′ N., 8° 46′ W.	10.30–11.00	1,050*	1,429	..	..	1,050*	1	2	..
25 (4)	50° 00′ N., 8° 47′ W.	13.35–14.05	2,075*	8,239	..	..	1,525*	..	25*	..
26 (4)	50° 01′ N., 8° 15′ W.	16.43–17.13	3,300*	520	..	..	3	1	..	..
27 (4)	50° 02′ N., 7° 44′ W.	19.53–20.23	587*	209	..	..	150*	1	4	..
28 (5)	50° 37′ N., 6° 54′ W.	01.35–02.05 Nt	334	1	..	..	270*	..	..	..
29 (5)	50° 42′ N., 6° 24′ W.	04.43–05.13 Dn	1,237*	11	..	..	18	3	..	..
30 (5)	50° 25′ N., 6° 17′ W.	08.35–09.05	6,075*	18	2,837*	50*	11	..	..	..
19–24 July.	Steam trawler *Elk*									
1 (19)	50° 01′ N., 4° 00′ W.	13.34–14.04	50*	1	18,350*	10	3	10	..	..
2 (19)	49° 42′ N., 3° 52′ W.	16.40–17.10	300*	4	7,320*	..	..	9	..	..
3 (19)	49° 22′ N., 3° 42′ W.	19.34–20.04	1,600*	6	3,620*	..	..	26	..	..
4 (19)	49° 19′ N., 4° 12′ W.	22.39–23.12 Nt	20*	5	460*	..	..	5	..	..

5 (20)	49° 15′ N., 4° 42′ W.	01.53–02.23 Nt	12	..	..	..	15	2	..	..
6 (20)	49° 11′ N., 5° 12′ W.	05.25–05.55 Dn	18	..	46	..	1	..	..	..
7 (20)	49° 06′ N., 5° 41′ W.	08.27–08.57	49	1	19	..	1	1	..	..
8 (20)	49° 03′ N., 6° 13′ W.	11.29–12.00	11	..	..	..	1	..	..	..
9 (20)	49° 06′ N., 6° 43′ W.	18.03–18.34	..	1	..	..	500*	..	1	..
10 (21)	49° 42′ N., 7° 23′ W.	00.42–01·12 Nt	1	..	55	..	180*	..	..	..
11 (21)	50° 03′ N., 7° 23′ W.	03.48–04.20 Nt	..	..	..	..	160*	..	..	..
12 (21)	50° 33′ N., 7° 09′ W.	07.32–08.02	..	1	5	..	..	..	..	..
13 (21)	50° 47′ N., 6° 56′ W.	10.44–11.15	5	3	1	..	..	..	..	..
14 (21)	51° 00′ N., 6° 32′ W.	13.54–14.24	5	3	..	..	..	..	..	..
15 (21)	51° 13′ N., 6° 08′ W.	17.06–17.36	..	1	..	..	1	19	..	..
16 (21)	50° 56′ N., 5° 50′ W.	20.39–21.11 Dk	300*	3	38,600*	100*	..	..	..	..
17 (21/22)	50° 37′ N., 5° 58′ W.	23.44–00.16 Nt	200*	5	950*	27	..	32	..	..
18 (22)	50° 17′ N., 6° 09′ W.	02.03–02.33 Nt	69	4	41	20*	29	49	..	..
19 (22)	50° 03′ N., 6° 16′ W.	05.10–05.40 Dn	12	5	69	60*	1	7	..	..
20 (22)	50° 02′ N., 6° 48′ W.	08.33–09.04	11	4	..	..	..	..	..	..
21 (24)	49° 42′ N., 6° 48′ W.	01.06–01.36 Nt	..	1	..	..	1,000*	46	..	..
22 (24)	49° 43′ N., 6° 17′ W.	05.00–05.32 Dn	..	1	..	..	..	7	..	..
23 (24)	49° 44′ N., 5° 45′ W.	08.35–09.05	50*	1	2,100*	..	2	1	..	..
24 (24)	49° 45′ N., 5° 13′ W.	11.50–12.20	600*	1	8,300*	50*	..	6	..	..
25 (24)	49° 59′ N., 4° 50′ W.	15.23–15.55	200*	2	3,950*	200*	..	10	..	..
26 (24)	50° 02′ N., 4° 22′ W.	17.49–18.19	800*	6	22,450*	50*	1	29	..	..

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15–18 March. Steam trawler *Elk*

1 (15)	50° 00′ N., 6° 55′ W.	11.44–12.18	..	..	..	..	700*	..	..	..
2 (15)	50° 03′ N., 7° 40′ W.	17.09–17.40	..	..	..	..	600*	..	..	..
3 (15)	50° 05′ N., 8° 29′ W.	21.45–22.15 Nt	..	..	..	..	1,950*	..	67	..
4 (16)	50° 07′ N., 9° 17′ W.	02.16–02.46 Nt	..	..	..	..	2,725*	..	95	..
5 (16)	50° 09′ N., 10° 00′ W.	06.42–07.12	4	..	..	..	175*	..	44	..
6 (16)	50° 10′ N., 10° 29′ W.	09.48–10.18	1	..	..	..	13	..	225*	1
7 (16)	50° 12′ N., 10° 57′ W.	12.48–13.18	118*	..	..	..	1	..	350*	..
8 (16)	50° 13′ N., 11° 31′ W.	16.01–16.32	7	..	..	..	1	..	850*	..
9 (16)	50° 14′ N., 12° 12′ W.	19.20–19.50 Dk	..	..	..	..	..	..	50*	..
10 (16)	50° 34′ N., 11° 34′ W.	23.18–23.48 Nt	..	..	..	..	..	..	300*	..
11 (17)	50° 52′ N., 9° 03′ W.	04.14–04.44 Nt	..	..	..	..	39	..	2,310*	42
12 (17)	51° 10′ N., 10° 23′ W.	08.40–09.10	..	..	..	..	4	..	185*	14
13 (17)	51° 10′ N., 9° 35′ W.	13.05–13.35	..	..	..	..	1	..	150*	4
14 (17)	50° 52′ N., 9° 03′ W.	16.23–16.53	..	..	..	..	78	1	435*	..
15 (17)	50° 43′ N., 9° 47′ W.	20.40–21.10 Nt	..	..	..	..	700*	..	750*	50
16 (18)	50° 33′ N., 10° 33′ W.	00.34–01.04 Nt	4	..	..	..	109	..	700*	43
17 (18)	50° 03′ N., 10° 29′ W.	04.45–05.15 Nt	6	..	..	..	354	..	690*	42
18 (18)	49° 49′ N., 9° 46′ W.	10.05–10.35	..	..	..	..	80	..	52	1
19 (18)	49° 52′ N., 8° 58′ W.	14.32–15.02	..	..	..	..	31	..	14	..
20 (18)	49° 55′ N., 8° 12′ W.	18.45–19.22 Dk	..	..	..	..	2,850*	..	1	..

TABLE VI (*cont.*)

Station number (date in parenthesis)	Station position	Time of haul (G.M.T.)	Mackerel eggs	Mackerel young stages	Pilchard eggs	*Muggiaea atlantica*	*Sagitta elegans*	*Sagitta setosa*	*Sagitta serrato-dentata*	*Sagitta lyra*
				1939						
16–27 April. S.S. *George Bligh*										
1 (16)	49° 50′ N., 4° 21′ W.	20.12–20.45 Nt	..	..	2,080*	..	420*	24	..	..
2 (17)	49° 18′ N., 4° 41′ W.	01.41–02.11 Nt	..	..	13,150*	..	11,440*	..	2	..
3 (17)	48° 50′ N., 4° 54′ W.	06.45–07.14	2	1	3	10	6,240*	38	111	..
4 (17)	48° 31′ N., 5° 05′ W.	10.15–10.45	..	..	..	17	2,480*	20*	45	1
5 (17)	48° 39′ N., 5° 30′ W.	13.49–14.19	17	..	..	12	2,700*	..	49	..
6 (17)	48° 47′ N., 5° 58′ W.	18.07–18.37	1,825*	..	50*	..	925*	..	..	..
7 (17)	48° 53′ N., 6° 27′ W.	22.24–22.52 Nt	797*	..	63*	..	1,203*	..	..	..
8 (18)	49° 00′ N., 6° 55′ W.	02.21–02.51 Nt	180*	..	510*	..	6,480*	1	1	..
9 (18)	48° 40′ N., 6° 48′ W.	06.04–06.35 Dn	9,000*	9	700*	..	32	..	1	..
10 (18)	48° 20′ N., 6° 40′ W.	09.40–10.10	2,725*	15	14,500*	6	63	..	20	1
11 (18)	48° 16′ N., 7° 07′ W.	15.16–15.46	1,625*	24	22,975*	..	15	..	46	4
12 (18)	48° 10′ N., 7° 35′ W.	22.14–22.44 Nt	9,850*	74	25*	1	400*	..	575*	4
13 (19)	48° 32′ N., 7° 38′ W.	02.06–02.37 Nt	8,025*	24	200*	..	525*	..	85	18
14 (19)	48° 53′ N., 7° 45′ W.	05.49–06.19 Dn	775*	1	25*	..	4	..	14	..
15 (19)	49° 19′ N., 7° 47′ W.	09.24–10.01	55*	..	440*	..	18	..	1	..
16 (19)	49° 10′ N., 8° 20′ W.	13.46–14.17	195*	..	20*	..	14	..	4	1
17 (19)	49° 06′ N., 9° 05′ W.	20.20–20.50 Nt	21,425*	7	125*	..	850*	..	150*	..
18 (20)	49° 05′ N., 9° 53′ W.	00.47–01.17 Nt	11,950*	7	..	..	42	..	20	1
19 (20)	49° 05′ N., 10° 26′ W.	04.24–04.55 Dn	15,225*	7	..	..	18	..	21	1
20 (20)	49° 21′ N., 10° 48′ W.	07.59–08.29	105	38	..	..	3	..	184	15
21 (20)	49° 40′ N., 11° 10′ W.	11.05–11.35	375*	33	..	..	1	..	1,510*	115
22 (20)	49° 44′ N., 10° 39′ W.	16.27–16.57	33,025*	174	..	..	..	..	30	5
23 (20)	50° 01′ N., 10° 18′ W.	19.58–20.28 Dk	12,000*	64	..	..	35	..	46	..
24 (20)	49° 47′ N., 9° 57′ W.	23.25–23.55 Nt	45,025*	4	..	..	175*	..	125*	..
25 (21)	49° 36′ N., 9° 30′ W.	02.45–03.15 Nt	5,950*	..	..	..	175*	..	11	1
26 (21)	49° 28′ N., 9° 04′ W.	06.04–06.34 Dn	10,300*	5	200*	..	..	..	..	..
27 (21)	49° 55′ N., 9° 10′ W.	11.25–11.57	4,050*	..	..	..	..	..	1	1
28 (21)	49° 51′ N., 8° 40′ W.	14.49–15.27	2,275*	..	..	..	..	..	..	..
29 (21)	49° 47′ N., 8° 10′ W.	18.29–18.59	1,260*	..	20*	..	2	..	..	..
30 (21)	49° 42′ N., 7° 42′ W.	22.10–22.40 Nt	29	..	2	..	1,250*	..	..	..
31 (22)	50° 02′ N., 7° 42′ W.	02.12–02.42 Nt	260	..	..	..	5,525*	..	..	..
32 (22)	49° 48′ N., 6° 43′ W.	07.04–07.34	9	..	49	..	1	2	..	..
33 (22)	49° 46′ N., 6° 11′ W.	10.42–11.12	..	..	710*	..	27	..	..	..
34 (22)	49° 45′ N., 5° 40′ W.	No haul								
35 (22)	49° 25′ N., 5° 40′ W.	18.49–19.19	70*	..	130*	2	3	..	..	..
36 (22)	49° 07′ N., 5° 37′ W.	22.47–23.17 Nt	98	..	..	2	2,500*	5	43	..
37 (23)	49° 15′ N., 6° 24′ W.	05.54–06.24 Dn	..	1	23,500*	..	..	..	..	..
38 (23)	49° 25′ N., 7° 08′ W.	12.06–12.36	87*	..	275*	..	67	..	..	..
39 (23)	49° 45′ N., 7° 14′ W.	16.17–16.47	290*	..	10*	..	..	..	..	..
40 (23)	50° 15′ N., 7° 22′ W.	21.35–22.05 Nt	245	..	..	..	1,850*	..	..	..

42 (24)	51° 14′ N., 7° 38′ W.	08.10–08.40	451	..	1	..	11	..	..	..
43 (24)	51° 34′ N., 7° 37′ W.	12.08–12.38	100*	..	..	..	..	..	..	..
44 (24)	51° 31′ N., 6° 46′ W.	17.05–17.35	125*	..	..	..	9	..	..	..
45 (24)	51° 28′ N., 5° 54′ W.	21.52–22.22 Nt	40*	..	..	..	162	1	..	..
46 (25)	51° 28′ N., 5° 22′ W.	01.33–02.03 Nt	..	..	..	..	1,100*	5	..	..
47 (25)	51° 08′ N., 5° 22′ W.	05.05–05.35 Dn	..	2	..	..	20	6	..	..
48 (25)	50° 48′ N., 5° 22′ W.	08.30–09.00	50*	1	..	..	5	5	..	..
49 (25)	50° 48′ N., 5° 53′ W.	12.15–12.45	1,250*	..	..	..	..	..	..	..
50 (25)	50° 49′ N., 6° 24′ W.	16.16–16.46	32	..	..	..	..	..	..	..
51 (25)†	50° 28′ N., 6° 40′ W.	19.47–20.17 Dk	65*	..	..	..	76	..	..	..
52 (25)†	50° 04′ N., 6° 31′ W.	22.36–23.06 Nt	70*	..	150*	..	1,575*	1	..	..
53 (26)†	49° 38′ N., 6° 48′ W.	01.53–02.24 Nt	65	..	9	..	800*	..	..	..
54 (26)	49° 33′ N., 6° 19′ W.	05.48–06.18 Dn	75*	..	1,700*	..	3	..	..	..
55 (26)	49° 20′ N., 6° 00′ W.	13.55–14.25	75*	..	92,925*	..	2	..	..	..
56 (26)	49° 40′ N., 5° 00′ W.	17.50–18.20	..	..	1,350*	..	2	3	..	..
57 (26)	50° 00′ N., 4° 38′ W.	21.35–22.05 Nt	..	..	13,100*	..	1	3	..	..
58 (27)	49° 26′ N., 4° 24′ W.	02.50–03.20 Nt	..	..	22,050*	..	168	..	..	..
59 (27)	48° 50′ N., 4° 10′ W.	07.45–08.15	20*	..	10*	2	350*	..	2	..
60 (27)	49° 02′ N., 3° 16′ W.	13.53–14.23	325*	..	4,175*	..	90	50	..	..
61 (27)	49° 32′ N., 3° 29′ W.	18.52–19.22	..	..	39,075*	..	8	8	..	..
62 (27)	50° 00′ N., 3° 45′ W.	22.20–22.50 Nt	..	..	60*	..	58*	183*	..	..
17–21 April. Fishery cruiser *Muirchu*										
SR **2913** (17)	51° 40′ N., 8° 00′ W.	12.00–12.30	..	..	..	..	..	..	..	..
SR **2914** (18)	51° 20′ N., 8° 00′ W.	12.30–13.00	37*	..	..	..	37	..	1	..
SR **2915** (18)	51° 00′ N., 8° 00′ W.	15.35–16.05	11	..	..	..	386	..	2	..
SR **2916** (18)	50° 40′ N., 8° 00′ W.	18.30–19.00	2	..	..	..	905*	..	6	..
SR **2917** (18)	50° 20′ N., 8° 00′ W.	21.45–22.15 Nt	..	..	..	..	2,626*	..	12	..
SR **2918** (19)	50° 00′ N., 8° 00′ W.	01.10–01.35 Nt	2	..	..	..	6,660*	..	2*	..
SR **2919** (19)	50° 00′ N., 8° 32′ W.	04.25–04.50 Dn	11	..	..	..	493*	..	14	..
SR **2920** (19)	50° 00′ N., 9° 00′ W.	07.35–08.00	88	..	..	..	..	..	..	..
SR **2921** (19)	50° 20′ N., 9° 00′ W.	10.40–11.10	54	..	..	..	..	..	2	..
SR **2922** (19)	50° 40′ N., 9° 00′ W.	13.50–14.20	9	..	..	..	21	..	35	..
SR **2923** (19)	51° 00′ N., 9° 00′ W.	16.50–17.20	28	..	26	..	..	..	1	1
SR **2924** (19)	51° 20′ N., 9° 00′ W.	19.42–20.12 Dk	23	..	..	..	..	..	..	1
SR **2925** (19)	51° 14′ N., 9° 42′ W.	23.25–23.55 Nt	694	..	..	..	135	..	2	1
SR **2926** (20)	50° 56′ N., 9° 55′ W.	02.45–03.15 Nt	9,570*	..	..	..	700*	..	1,024*	9*
SR **2927** (20)	50° 36′ N., 9° 55′ W.	06.10–06.40	38,958*	11	..	..	1	..	7	..
SR **2928** (20)	50° 16′ N., 9° 55′ W.	09.20–09.50	33,000*	120	..	..	..	..	..	..
SR **2929** (20)	50° 16′ N., 10° 26′ W.	12.40–13.10	11,700*	95	..	..	1	..	1	5
SR **2930** (20)	50° 16′ N., 10° 57′ W.	16.10–16.40	1,092*	13	..	..	..	..	29	..
SR **2931** (20)	50° 36′ N., 10° 48′ W.	19.24–19.54	480	73	..	..	6*	..	194*	20*
SR **2932** (20)	50° 56′ N., 10° 48′ W.	22.24–22.54 Nt	14	6	..	..	60*	..	467*	12*
SR **2933** (21)	51° 16′ N., 10° 48′ W.	02.00–02.30 Nt	5	41	..	..	91	..	1,305*	1
SR **2934** (21)	51° 33′ N., 10° 48′ W.	04.55–05.25 Dn	10	10*	..	..	84*	..	384*	..

† Owing to bad weather, the net was fished over the side while the ship drifted.

TABLE VI (*cont.*)

Station number (date in parenthesis)	Station position	Time of haul (G.M.T.)	Mackerel eggs	Mackerel young stages	Pilchard eggs	*Muggiaea atlantica*	*Sagitta elegans*	*Sagitta setosa*	*Sagitta serrato-dentata*	*Sagitta lyra*
				1939						
2–7 June.	Steam trawler *Elk*									
1 (2)	49° 50′ N., 4° 57′ W.	04.12–04.42 Dn	825*	..	121,950*	..	1	8	..	..
2 (2)	49° 29′ N., 5° 33′ W.	08.34–09.04	3,825*	20	12,475*	..	75*	Few	..	..
3 (2)	49° 08′ N., 6° 07′ W.	13.02–13.32	28,500*	52	675*	..	2,100*	300*	..	..
4 (2)	48° 47′ N., 6° 43′ W.	17.22–17.52	6,100*	337	..	..	950*	..	103	..
5 (2)	48° 26′ N., 7° 18′ W.	22.00–22.30 Nt	2,475*	440	..	450*	1,125*	..	600*	..
6 (3)	40° 05′ N., 7° 53′ W.	02.30–03.00 Nt	1,250*	57	50*	Numerous	..	..	350*	28
7 (3)	48° 32′ N., 8° 18′ W.	07.23–07.53	3,225*	634	..	Numerous	112*	..	50*	17
8 (3)	48° 58′ N., 8° 45′ W.	12.15–12.45	425*	43	..	Moderate	150*	..	75*	1
9 (3)	49° 25′ N., 9° 10′ W.	17.05–17.35	225*	148	..	Few	325*	..	62*	..
10 (3)	49° 50′ N., 9° 35′ W.	21.30–22.00 Nt	11	178	..	..	150*	..	Few	..
11 (4)	50° 17′ N., 10° 00′ W.	02.20–02.50 Nt	89	45	..	..	425*	..	287*	1
12 (4)	50° 42′ N., 10° 25′ W.	07.43–08.13	1,350*	45	..	..	2	..	31	7
13 (4)	51° 06′ N., 9° 27′ W.	13.55–14.25	9,525*	167	..	..	17	..	..	..
14 (4)	50° 40′ N., 9° 02′ W.	18.50–19.20	4,950*	40	..	..	..	..	..	..
15 (4)	50° 14′ N., 8° 36′ W.	23.20–23.50 Nt	650*	284	..	..	100*	..	2	..
16 (5)	49° 49′ N., 8° 12′ W.	04.15–04.45 Dn	1,850*	27	..	..	325*	..	..	..
17 (5)	49° 23′ N., 7° 46′ W.	08.55–09.25	5,900*	183	..	..	..	..	..	..
18 (5)	49° 07′ N., 7° 30′ W.	16.15–16.45	4,350*	134	..	..	250*	1	4	..
19 (5)	49° 35′ N., 6° 39′ W.	22.24–22.54 Nt	10,725*	227	450*	..	2,175*	1	..	..
20 (6)	50° 00′ N., 7° 04′ W.	03.15–03.45 Nt	1,800*	1	25*	..	81	..	..	..
21 (6)	50° 25′ N., 7° 29′ W.	07.43–08.13	6,760*	7	..	..	7	..	..	..
22 (6)	50° 50′ N., 7° 55′ W.	12.15–12.45	12,075*	3	..	..	116	..	..	..
23 (6)	51° 14′ N., 8° 20′ W.	16.15–16.45	8,550*	65	..	..	9	..	..	..
24 (6,	51° 14′ N., 7° 32′ W.	21.00–21.30 Dk	8,750*	9	..	..	25	1	..	..
25 (7)	51° 15′ N., 6° 47′ W.	01.20–01.50 Nt	8,700*	6	..	..	825*	1	..	..
26 (7)	50° 45′ N., 6° 38′ W.	05.50–06.20	6,000*	59	..	..	2	2	..	..
27 (7)	50° 16′ N., 6° 29′ W.	11.08–11.38	2,250*	7	50*	..	10	..	..	..
28 (7)	49° 58′ N., 5° 47′ W.	14.32–15.02	6,150*	3	73,050*	..	..	2	..	..

SOME NOTES ON PARASITIC COPEPODA

By Robert Gurney, D.Sc.

(Text-figs. 1–2)

Developmental Stages in the Family Lernaeopodidae

The Lernaeopodidae are a highly specialized group of parasitic Copepoda presumably derived from a Caligoid stem, and some clue to their systematic position should be found in their development. Some stages are known in ten genera, but it is only in *Achtheres*, *Salmincola*, and *Clavella* that the whole, or nearly the whole, series of stages has been described. There is a very strong tendency to suppress the nauplius as a free stage though, when so suppressed, there may be moults corresponding to nauplius and metanauplius (Zandt, 1935). In some species there is certainly a free nauplius, but it probably moults into the copepodid in a very short time.

With free nauplius	Hatching as copepodid
Achtheres percarum Nordmann	*Achtheres ambloplitis* Kellicott (normally)
	A. pseudobasanistes Zandt [Syn. *Basanistes coregoni* Neresh.]
Tracheliastes polycolpus Nordmann	*Salmincola salmonea* (L.)
	Salmincola mattheyi Dedie
Clavella uncinata (Müller)	*Salmincola edwardsi* Olsson
Charopinus dalmanni (Retz.)	*Basanistes huchonis* (Schrank)
Lernaeopoda galei Kröyer	*Epibrachiella impudica* (Nordmann)

I am indebted to Miss Lebour for larvae of *Lernaeopoda galei* hatched in the laboratory at Plymouth (Fig. 1). In this species there is a nauplius, but it probably moults almost at once into the copepodid as all the appendages of the latter can be seen under the skin, and the head filament is quite distinct. One interesting feature of the nauplius is the possession of a mandibular appendage, since in all other species in which a nauplius has been described this appendage is absent altogether. In this species the appendage is, at the time of hatching, empty of tissues, but it is distinctly biramous, with three long setae on the exopod and two on the endopod. Both pairs of antennae have long setae, but they are not feathered, and it may well be that the nauplius does not actually swim.

The copepodid (0·85 mm. long) is slender, but of the usual form. The filament of attachment is fully formed, running backwards to the region of the maxillipede, where it is thrown into a double coil and then runs forwards again to just below the attachment disk. The mouth cone is large, consisting of a bifid lower lip and an upper lip quite distinct from it. The lower lip has a fringe of delicate hairs at the tip, but it is not easy to see, and it may actually be a finely striated membrane. The mandibles lie outside the cone and are simple stylets, but I have seen a minute papilla at the base which may be a vestige of an exopod. The maxillule has two lobes with two and three spines respectively. Maxilla and maxillipede are powerful prehensile organs, the former with a slender claw and the latter with a more massive curved claw, in this respect quite unlike *Clavella* and *Epibrachiella*, and more resembling *Salmincola*. Nothing is known about later stages.

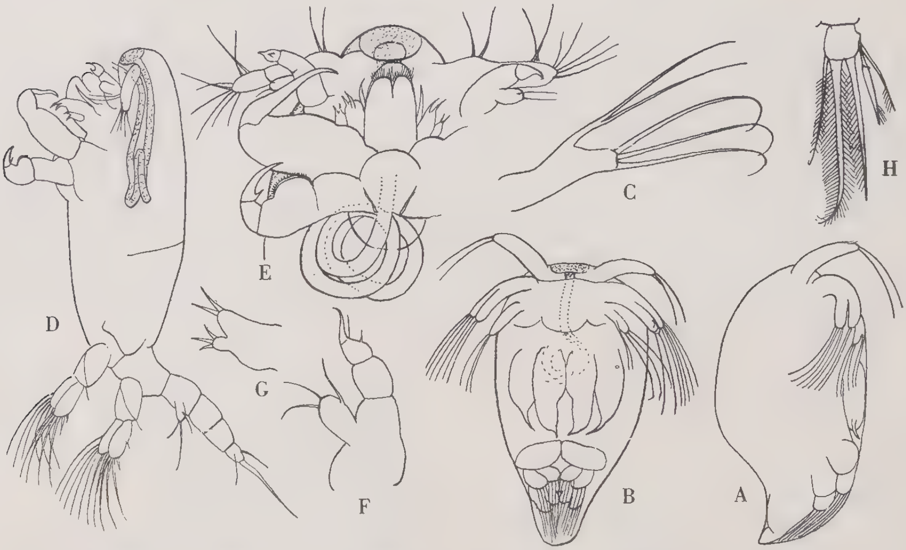

Fig. 1. *Lernaeopoda galei*. A, B, nauplius; C, mandible of nauplius; D, copepodid; E, head region of copepodid, ventral view; F, antenna of copepodid; G, maxillule of copepodid; H, left furcal ramus, ventral view.

There have been three recent papers dealing with the development of Lernaeopods (Zandt, 1935; Dedie, 1940; Friend, 1941) and it is remarkable that there are apparently very great differences in the series of stages. According to Zandt there are no less than six moults, and seven stages in all, which is one more moult and stage than in the development of the free-swimming copepods. Throughout these moults no new appendages are acquired, and the animal remains throughout at the same developmental grade as copepodid 1 of normal free-swimming Copepoda.

In Table I the series of stages in four species are summarized, and it will be seen that there is a progressive shortening of development. In *S. salmonea*, according to Friend, there are only three moults, and the female has a stage during which she is attached to the host only by the grasping maxillipedes. In *Clavella* there appear to be not more than three moults, and it is possible that the female has a very brief period of freedom after loosing from the head filament and before attachment by the bulla or maxillary disc.

TABLE I. DEVELOPMENTAL STAGES IN FOUR LERNAEOPODS

	Achtheres pseudobasanistes Zandt	*Salmincola mattheyi* Dedie	*Salmincola salmonea* (L.)	*Clavella uncinata* Müller
Observer:	Zandt, 1935	Dedie, 1940	Friend, 1941	Gurney, 1934
Stage I	Copepodid 1: free, later attached by head filament	Copepodid 1: the same	Copepodid 1: the same	Copepodid 1: the same
II	Copepodid 2: attached by head filament, legs reduced	Metamorphosed; filament detached from head and grasped by maxillae	Filament detached from head and grasped by maxillae	Copepodid 2: legs reduced, attached by head filament
III	Filament detached from head and grasped by maxillae	Ditto	Metamorphosed; 1st stage female free, clinging by maxillipedes	Metamorphosed; attached by filament and skin of copepodid
IV	Ditto	Ditto	2nd stage female, attached by bulla	Sexes distinct, female attached by bulla
V	Ditto (Legs still traceable)	Sexes distinct; female fertilized, still attached by filament	—	—
VI	Approaching adult form; sexes distinct; still fixed by filament	Female attached by bulla	—	—
VII	Male free, female fixed by bulla. No further moult	—	—	—

THE COPEPODID STAGE OF THE EYE-MAGGOT OF THE SPRAT *LERNAEENICUS SPRATTAE* (SOWERBY)

Leigh-Sharpe (1935) has recorded the occurrence of this species in the spring of 1934 on about 3% of the sprats caught at Hole's Hole in the river Tamar near Plymouth. On 10 April of the same year I found the same percentage of infection on sprats from Hole's Hole, young herrings taken in the same place being entirely free from the parasite. Leigh-Sharpe does not give the actual date of his catch, but it is remarkable that, while his specimens were mature and bearing eggs, not one of mine was full-grown or bore eggs. In no instance was more than one parasite found on one fish. In one specimen a hole was seen in the eye, but no parasite emerging, and on dissection the chitinous remains of an adult specimen were found embedded in a cyst in the eyeball. Sproston & Hartley (1941) found a very much lower percentage of infection of sprats in the Tamar during 1935 and 1936, namely 0·655% among 1376 fish taken throughout the year.

The youngest stage found corresponded to the free-swimming adult stage of *Lernaeocera branchialis* (L.), and was about 3 mm. long, with a part of the abdomen projecting from the hole in the fish's eye, and the head embedded in the tissues at the back of the eye. It is to be presumed that the specimen figured (Fig. 2) is actually the earliest stage in which the fish is attacked. It would seem probable that it does not pierce the eyeball until the abdomen is long enough to project through the hole made while the head reaches to the back of the eye. The proportion of length of abdomen to cephalothorax is about the same as that in some specimens of *L. branchialis* still attached to the gill of a flounder. While the animal is sufficiently provided with organs of

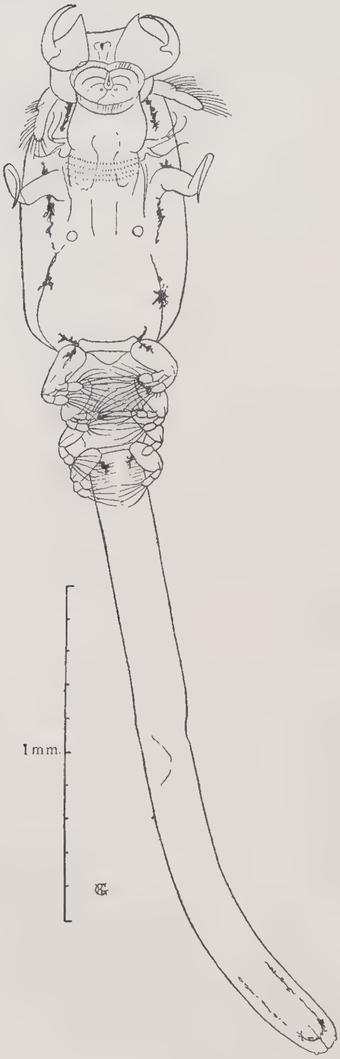

Fig. 2. *Lernaeenicus sprattae* Sowerby. Young specimen from eye of sprat.

prehension, the circlets of spinules at the base of the mouth cone may also assist in fixation.

I have not found any earlier stages on the body, fins or gills of the sprat, but the number examined is very small and, in view of the rarity of the copepod, the possibility that the early stages are passed on some part of the same host cannot be excluded. I have found none on the gills of a flounder which bore large numbers of larvae of *L. branchialis*.

While it is easy to follow every stage of development on the sprat from the time of attachment to the eye, nothing is at present known about the copepodid stages.

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THE ANTHEROZOIDS OF *DICTYOPTERIS*

By T. Johnson

Dublin

I should like to place on record the circumstances under which I saw for the first time that the male cells of the *Dictyota* family were not non-motile spermatia but ciliated motile antherozoids.

With the help of a grant from the Royal Society I spent two long vacations (in 1885 and 1886) investigating the marine algae of Plymouth Sound and district, thanks to the facilities provided for such work by the Marine Biological Station at Plymouth. It was usual to spend the morning collecting material by dredging or shore work, sorting it out in the afternoon, and returning for microscopic examination of selected material in the evening. Dredging off the Eddystone yielded male plants of *Dictyopteris* and examination of one piece showed an antheridium in course of breaking up. The contents scattered in all directions as motile bodies starting at the lower right corner, as looked at, and passing gradually to the upper left corner. I never saw anything more clearly under the microscope. I put material in absolute alcohol for further examination but unfortunately did not keep the microscopic specimen or fix the antherozoids with iodine. When I showed my chief (Dr D. H. Scott) my account of the discovery he expressed the opinion, to which I naturally deferred, that it would be incautious to publish anything so startling, based on one observation, and, in consequence, in the published account I spoke of indications that the male cells would prove to be motile. Later on my former pupil Williams (1904) proved the bi-ciliated nature of spermatozoids in the Dictyotales by using material kept in a moist chamber.

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THE PORTUGUESE MAN-OF-WAR, *PHYSALIA PHYSALIS* L., IN BRITISH AND ADJACENT SEAS

By Douglas P. Wilson, M.Sc., F.R.P.S.

Zoologist at the Plymouth Laboratory

(Plates I–III and Text-figs. 1–5)

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THE OCCURRENCE OF *PHYSALIA* ON THE ATLANTIC COASTS OF EUROPE

Past Records

The occurrence of the Siphonophore *Physalia physalis* L. (Portuguese Man-of-war) in large numbers off our south-western shores in the summer and autumn of 1945 was an event almost without parallel in the records for British seas. A search of the literature for the last 100 years or so has produced only the recorded occurrences listed in Table I in which are included strandings on the northern and western coasts of France and of Belgium. The list also includes some hitherto unpublished records preserved at the Plymouth Laboratory; these are discussed in detail below.

TABLE I. LIST OF STRANDINGS OF *PHYSALIA* ON THE SHORES OF THE BRITISH ISLES, NORTHERN AND WESTERN FRANCE AND BELGIUM

Year	Season or month	Locality	Number	Wind	Reference
1834	March	Ardmore, Co. Waterford	One	—	Thompson (1835)
1852	—	La Rochelle	Several, at least	S.-S.W. persistent	De Quatrefages (1854)
1862	Aug.	Isle of Wight	Hundreds	After gale	Rogers (1862)
1862	Summer	Torbay, S. Devon	Three	—	Gosse (1865)
1884	Sept.	Dunkerque	One dead	After storm	Théry (1887)
1907	May	Valentia	One	—	Delap (1924)
1907	Aug.	At sea, 50° 16′ N., 11° 27′ W.	One	—	Stelfox (1936)
1912	March	Roscoff	One	—	de Beauchamp (in Caullery, 1912)
1912	April	Boulogne	Dozen	After westerly gales	Caullery (1912)
1912	April	Knocke (Belgium)	Three	After westerly gales	Lameere (1912)
1912	March–April	Seaford, Rye, etc. to Ilfracombe	Thousands	After strong south to south-westerly winds	This paper
1913	Feb.–April	Bigbury Bay, Plymouth Sound, Looe, and Aberystwyth	Several	After strong south to west winds	This paper
1919	—	Guéthary	Numerous	—	Pérèz (1929)
1921	Jan.	Bantry, Co. Cork	Great shoal	—	Delap (1924)
1934	Oct.–Nov.	Perranporth to Polzeath, N. Cornwall	Several	After strong south to west and north-west winds	This paper
1934	Autumn	Hook Tower Lighthouse, Co. Wexford	One	—	Stelfox (1936)
1934	Nov.	Tragumina, Co. Cork	One	—	Stelfox (1936)
1935	Oct.	Hook Tower Lighthouse, Co. Wexford	One	—	Stelfox (1936)
1935	Oct.	Mullion Cove, S.W. Cornwall	One	After westerly winds	This paper
1935	Nov.	Newquay, N. Cornwall	One	After strong westerly winds	This paper
1945	July–Oct.	Cornwall, Devon, S. and N. Wales, Eire	Large shoals	Fully discussed below	This paper
1945	July–Oct.	Roscoff	Several	—	Bocquet (private communication)
1945	Aug.–Sept.	Concarneau	Large numbers	—	Bouxin & Legendre (1946)
1945	Dec.	Mousehole, Cornwall	Three	After S.W. gale	This paper
1946	Jan.	Whitsand Bay, Cornwall and Penzance	A few	After S.W. gale	This paper
1946	July–Sept.	Guéthary to La Rochelle	Enormous swarm	—	Weill (1946)

Only in 1862 and 1912 does there appear to have been anything comparable with the strandings of 1945. On 7 August 1862 hundreds of *Physalia* were washed ashore on the Isle of Wight (Rogers, 1862) but data for other parts of the coastline do not exist apart from three specimens seen near Torquay that summer (mentioned by Gosse, 1865, p. 256). For 1912 there are very few published data (Caullery, 1912 and Lameere, 1912) but whilst endeavouring to check a reference to strandings under this Laboratory (*Plymouth Marine Fauna*, 1931, p. 84) I found some correspondence relating to the occurrence of *Physalia* in great abundance that year. They were seen at points along the south coast westwards from Rye Bay to the Isles of Scilly and northwards to Aberystwyth during the months of March and April. With the correspondence was the typescript of an unpublished article by Professor J. H. Orton, then a naturalist on the staff of this Laboratory. There were also a few further records for strandings in 1913 and these are listed below together with those for 1912.

Table II. Records of Strandings of *Physalia* on the shores of England and Wales in 1912 and 1913

1912	Locality	Number	Observer
	A. South Coast Series		
? March	Isles of Scilly	—	Mr Ritchie
9 and 10 March	Plymouth Sound	—	Mr (now Professor) J. H. Orton
12 March	Bigbury Bay, Devon	Thousands	Mr F. Chandos-Pole
? March	Looe, Cornwall	—	Mr C. H. Drew
23 March and subsequently	Seaford, Sussex	Very many	Mr S. F. Maurice Dauncey
3 April	Rye Bay, Sussex	One	Mr F. Slade
	B. West Coast Series		
17 March	Thurlestone Sand, near Aberystwyth, Cardigan	Several	Mr C. L. Walton
20 March	Cardigan Bay	One	Mr H. J. Fleure
2 and 3 April	Ilfracombe, N. Devon	Many	Mr E. S. German
1913			
10 Feb.	Looe, S. Cornwall	Several	Dr A. Adams
17 March	Aberystwyth, Cardigan	One	Mr C. L. Walton
23 March	Bigbury Bay, S. Devon	Several	Mr F. Chandos-Pole
25 March–2 April	Plymouth Sound	Several	Mr (now Professor) J. H. Orton

Credit for several of the records in 1912 is due to Mr W. R. Adams of Camberwell, London, who wrote to several of his friends on the coast and thereby produced the records for Seaford, Rye and Ilfracombe. On 3 April 1912 he received in London twenty-four living *Physalia* from Ilfracombe; although battered they were placed in the sea-water aquarium of the Horniman Museum where they survived a short while. Mr Adams also got one of his friends to search at Dover but no *Physalia* was found there. He mentions in a letter dated 6 April 1912 that a correspondent writing to *Country Life* stated that the species was washed up at Bognor.

The records for 1934 have not previously been published. They refer to several specimens stranded between Perranporth and Port Isaac on the north coast of Cornwall from 30 October to 12 November. Some of the specimens were sent to the Plymouth Laboratory for identification.

TABLE III. RECORDS OF STRANDINGS OF *PHYSALIA* IN NORTH CORNWALL IN 1934

1934	Locality	Number	Observer
30 Oct.	Perranporth	One	Mr N. Light
3 Nov.	Polzeath	Several	Mrs B. C. Peirson
5 Nov.	Padstow district	Several	Mr A. G. Blaydes
First week Nov.	Newquay	One	Mr F. S. Russell
12 Nov.	Port Isaac	Two	Mr R. A. Todd

On 18 October 1935 a specimen picked up at Mullion Cove was sent to this Laboratory by Miss E. M. L. Hendriks and on 3 November in the same year another one was seen on Fistral Beach, Newquay, by Mr F. S. Russell. Both these records are here published for the first time; they are included in Table I.

The 1945 records are listed in Table IV and discussed in detail below. Since their occurrence Weill (1946) has recorded an enormous swarm of large *Physalia* on the beaches of south-west France from Guéthary to La Rochelle from the end of July to the end of September 1946. So far as I have been able to ascertain there are no English records for this period.

In addition to the above definite records there are a few other references to be noted. De Quatrefages (1854) obtained specimens at La Rochelle which enabled him to make his extensive studies on the organization of *Physalia*. Gosse stated (1865, p. 255) that 'scarcely a season passes without one or more of these lovely strangers occurring in the vicinity of Torquay'. Perhaps they were more frequent in his day than they are now. In a note to Théry's paper (1887) Giard states that Beltremieux in his *Fauna de la Charente Inférieure* indicates that *Physalia* is found very rarely at La Rochelle and that Lafont has seen it at Arcachon, but no dates are given. Vanhöffen (1906) says that Owen saw it on the coast of Cornwall and McIntosh at Southport and the Hebrides, but gives no references and I have not been able to find them.

It is evident from the above that *Physalia* may be expected to reach French Atlantic and English shores from time to time after absences of several years, but that strandings in great abundance are only likely to take place three or four times in a century. They can arrive in any season of the year. Those who have recorded the presence of *Physalia* have generally referred to stormy weather or to strong or persistent winds from the south to west quadrant preceding the strandings, and this question will be discussed in a later section.

Two points may be made now. If the dates for the main occurrences this century be examined there is a suggestion of an 11-year periodicity, 1912 (no records for 1923), 1934, 1945, close to the sun-spot minima. The remainder of the records, particularly those for the nineteenth century, however, do not seem to bear this out, they do not have a similar periodicity or correspondence with sun-spot activities.

Another feature to be noted is the frequent occurrence of *Physalia*, generally in smaller abundance, the year following a main invasion; thus 1946 after 1945, 1935 after 1934, 1913 after 1912. It suggests that an abundance one year is likely to be followed by further, though fewer, specimens the next.

THE 1945–46 RECORDS FOR THE BRITISH ISLES

On 31 July 1945 there appeared in *The Times* a letter from Professor J. H. Orton recording the capture of a *Physalia* at Trevone, north Cornwall and requesting the forwarding to him of any further specimens that might be found. On the same day we received at the Plymouth Laboratory a preserved specimen from Major A. A. Dorrien Smith, Tresco, Isles of Scilly taken by him a few days previously; he stated that he first saw the species floating at sea on 2 July. On 3 August we received from him a living specimen in first-class condition; this specimen was kept alive for several days enabling a series of photographs to be taken, three of which are reproduced on the plates accompanying this paper. A set of photographs and an article were despatched on 7 August to *The Illustrated London News* with the aim of calling attention to the presence of *Physalia* in our waters and reinforcing Professor Orton's appeal for specimens and records. The article was not published until 1 September but it had the effect of re-stimulating interest just as the response to *The Times* letter was dying down. Both Professor Orton and I received numerous letters and several specimens and he has very kindly handed all his correspondence over to me and I am therefore able to deal with the observations as a whole.

This is probably the first time that such a complete set of records of the strandings of a subtropical organism on our shores has been got together. Whilst obviously many must have gone unrecorded, for not every one sees the particular newspaper and periodical mentioned, or would take the trouble to write had they done so, it can, I think, be safely assumed that the records do give a fair sampling of the distribution of the *Physalia* and that with the exception of Eire an absence of reports does indicate a real absence of the siphonophore. On that basis the reports will be discussed.

Below is a list of records in order of dates of finding as closely as the correspondents gave them together with their own estimate of the numbers involved. Few gave an estimate of size but from those who did, and from the specimens sent, it is obvious that the pneumatophore length varied from about 2 in. to about 9 in. (5–23 cm.). There is no doubt at all that apart from damage due to stranding the *Physalia* were in excellent condition and those seen at sea

TABLE IV. LIST OF STRANDINGS OR SIGHTINGS AT SEA OF *PHYSALIA* DURING THE SUMMER AND AUTUMN OF 1945 AND EARLY 1946

Date (1945)	Locality	Number	Observer
2 July	Isles of Scilly	One	Major A. A. Dorrien Smith
Early July	Sennen Cove, Cornwall	One	Mr G. L. Norris
End of first week	Sennen Cove, Cornwall	One	Mr W. Finsbury
6 July	Isles of Scilly	One	Mrs Wakefield
14 July	Polzeath, Cornwall	One	Mrs Robert Fraser
Mid-July	Isles of Scilly	Several	Major A. A. Dorrien Smith
20–30 July	Porthgwarra, near Porthcurno, Cornwall	Five	Mr Donald Boyd
22 July	St Ives Bay, Cornwall	One	Mrs Mary Riley
24 July	Trevone, Cornwall	One	Prof. J. H. Orton
25 July	Isles of Scilly	One	Major A. A. Dorrien Smith
28 July	Isles of Scilly	One	Major A. A. Dorrien Smith
28 July	Trevose Head, Cornwall	One	Miss H. J. Wilkins
29 July	Crantock Beach, near Newquay	One	Miss D. M. Wilde
30 July	Port Isaac, Cornwall	Two	Mr P. W. S. Andrews
31 July and previous four days	St Ives, Lelant Beach, Cornwall	One Six	Mrs Denise M. Hinckley
31 July	Penzance, Cornwall	Many	Prof. Hugh Sellon
31 July	Polzeath, Cornwall	One	Mrs Robert Fraser
Last week in July	Isles of Scilly	Several hundreds	Mr John Craxton
1 Aug.	St Ives, Cornwall	Three, but numerous in district	Mr A. Naysmith
1–7 Aug.	Isles of Scilly	Seen daily, several	Cadet H. Wakefield
2 Aug.	Near the Bishop Light	Quite eight or ten	Major A. A. Dorrien Smith
3 Aug.	Isles of Scilly	One	Major A. A. Dorrien Smith
3 Aug.	St Ives, Cornwall	Five, but there were a number of others	Master Oliver Hinckley
5 Aug.	Godrevy Beach, St Ives, Cornwall	One	Mrs V. Alport
5 Aug.	Crantock Beach, Newquay, Cornwall	One	Miss D. M. Wilde
6 Aug.	Carbis Bay, St Ives, Cornwall	Two	Miss Phyllis M. Angove
Beginning of Aug.	Nevin, N. Wales	Two	Honours Student of Prof. Brambell
6 Aug.	Perranporth, Cornwall	One	Mr Bernard D. Burch
7 Aug.	St Ives, Cornwall	One	Mrs V. Alport
7 Aug.	Lundy Cove, Portquin Bay, Cornwall	Four	Miss Rosalind Fraser
13 Aug.	Isles of Scilly	Two	Major A. A. Dorrien Smith
20 Aug.	Trevone, Cornwall	Two	Mr Edward M. James
23 Aug.	Watergate Beach, Cornwall	One	Miss Mary Stokes
24 Aug.	Sennen Cove, Cornwall	Two	Captain A. Carter
25 Aug.	Croyde Bay, Devon	One	Mr A. A. N. Gardener
25 Aug.	Westward Ho, Devon	Three	Master G. A. Young
Last week of Aug.	Nantrum end of Croyde Bay, Devon	Three	Mr G. H. Jenkins
28 Aug.	Seven Stones, Isles of Scilly	Several	Major A. A. Dorrien Smith
29 Aug.	Off Wolf Lighthouse	One	Mrs Wakefield
31 Aug.	Wolf Rock	One (four or five the previous day)	Mr P. H. T. Hartley
1 Sept	Tenby, S. Wales	Two	Lieut. J. N. Atkinson
2 Sept.	Tenby, S. Wales	Several	Mr B. R. Symes
2 Sept	Isles of Scilly and to westward	Quite a number	Major A. A. Dorrien Smith

TABLE IV (*cont.*)

Date (1945)	Locality	Number	Observer
arly Sept.	Caldy Island, S. Wales	One	Dr Colin Mathieson
arly Sept.	Tenby, S. Wales	Six	Dr Colin Mathieson
econd week of Sept.	Bigbury Bay, S. Devon	Two	Lieut.-Com. E. G. Beazley
Week prior to 16 Sept.	At sea, near Dartmouth	One	Mr. W. J. Wallis
Week before 17 Sept.	St Mawes, S. Cornwall	Several	Mr V. Heather
Mid-Sept.	Land's End, Cornwall	Numerous	Prof. Hugh Sellon
econd and third week Sept.	Lizard, S. Cornwall	Several	Miss G. M. Puyer
5 Sept.	Porth Nanven, near Land's End, Cornwall	Two	Mr P. H. T. Hartley
7 Sept.	Mill Bay, near Land's End	Scores	Mr Lawrence Leith
On or about 17 Sept.	Mousehole, Penzance	A number	Miss Ruth Adams
7 Sept.	Druidston, near Haverfordwest, Pembroke	One	Mr A. N. Grace
8 Sept.	Manorbier, Tenby, S. Wales	One	Miss Gladys Flynn
9 Sept.	St Anthony, S. Cornwall	Three	Mr E. C. Richards
9–23 Sept.	Annestown, near Tramore, Co. Waterford	Considerable numbers	Miss M. A. Walker
3 and 24 Sept.	Woolacombe Bay, Devon	Twenty-seven, and must be others	Mrs Evelyn J. H. Pollard
3 Sept.	Widemouth Bay to Hartland Bay, Bude Bay	Very many	Mr C. D. Barrett
4 Sept.	Croyde Beach, Devon	One	Mrs E. L. Balmer
4 Sept.	Porth Headland, near Newquay, Cornwall	Four	Mr R. S. Funnell
ept.	Bude, Cornwall	Several	Mrs Elsie E. Sampson
5 Sept.	Land's End, Cornwall	Still coming ashore	Prof. Hugh Sellon
5 and 26 Sept.	Combe Martin and Heddon's Mouth, Devon	One at Coombe Martin, two at Heddon's Mouth	Mr J. Hobart
and 27 Sept.	Borth, Cardiganshire	Many	Mrs A. M. Nicholson
out 25 Sept.	St Bride's Bay, Pembroke	One	Dr Colin Mathieson
6 Sept.	Borth, Cardiganshire	Three	Mrs M. Franks
Sept.	Trevone, Cornwall	Five	Dr R. M. Boveri and Mr W. M. Lindley
7 Sept.	Rhosneighr, Anglesey	Ten or so	Mr. P. M. A. Plews
7 Sept.	Cheyne Beach, Ilfracombe	Two	Mr A. S. Cutcliffe
8 Sept.	Westward Ho, Devon	Two	Col. G. H. Young
Sept.	Fistral Bay, Newquay	Four	Mr F. S. Russell
nd of Sept.	Bude, Cornwall	Several	Mr E. G. Ricketts
nd of Sept.	Perranporth, Cornwall	Hundreds in the sea	Mrs M. Stuart
4 Oct.	Gwenver Beach, near Land's End, Cornwall	One	Mr P. H. T. Hartley
0 Oct.	Isles of Scilly	Several	Major A. A. Dorrien Smith
Mid-Oct. to late Oct.	Ballyteige Burrow, S. Wexford	Fairly plentiful, one every ½ mile or so	Mr W. J. Scallan
1 Oct.	Rhosneighr, Anglesey	Two	Mr P. M. A. Plews
0 Dec.	Mousehole, Cornwall,	Three	Mrs E. Pearce
1946			
2 Jan.	Whitsand Bay, S. Cornwall, near Plymouth	One	Mrs Hawkes
3 Jan.	Gwenver Beach, Penzance	A few	Mr T. G. Wm. Fowler

in full health and vigour and not feeble or dying. Several persons were severely stung, some whilst bathing, and bore testimony to the pain inflicted. Miss M. A. Walker, who in addition to writing to me published her observations, has an amusing note (Walker, 1946) that the 'local people at Annestown were convinced that the balloon-like floats of *Physalia* had poison gas in them and gave them a very wide berth'. Whenever they were stranded in any numbers they aroused much interest among the general public who were attracted by the brilliance and beauty of the colouring.

METEOROLOGICAL CONSIDERATIONS

Physalia is blown along by the wind which seems to have a greater influence on its movements and distribution than the ocean currents. It is to the winds that we should first look in attempting to account for the recurring invasions of our seas by these oceanic organisms of lower latitudes.

Past Records

The references to past strandings have generally been accompanied by mention of strong winds from south to west. Thus de Quatrefages (1854) says that his specimens collected at La Rochelle in 1852 arrived after persistent winds from the south or south-west. In 1862 Rogers refers to a 'terrific gale' and Théry (1887) to 'quelques jours d'un vent assez violent' in September 1884.

For 1912 we have Caullery's statement that preceding the strandings in April 'l'hiver et le début du printemps dernier se sont signalés sur nos côtes de la Manche par des tempêtes d'ouest répétées' and Orton, in the unpublished article already referred to says: 'There can be little doubt that the presence of *Physalia* on the south coast of England in March and April 1912 was due to the almost continuous southerly to south-westerly winds indicated in the eastern part of the Atlantic in the Meteorological Reports for the early part of that year.' This I have checked from the Daily Reports for 1912; they show a great preponderance of strong (Beaufort Scale 4–7) south to west winds throughout the last three weeks of February and most of March in the region of Scilly. From the end of March and in early April the winds were mainly west to north and again strong. From about 12 April for the rest of the month the winds were mainly light with an easterly component between south and north and with north-east and south-east winds frequent. Probably this change of wind was responsible for the disappearance of *Physalia* from the area after the first few days of April. Orton goes on to say: 'It is interesting to note that at the end of March northerly winds set in in the eastern part of the English Channel. This circumstance probably explains why *Physalia* and *Velella* were driven on to the French side of the Straits of Dover.'

The 1913 strandings, which were nothing like as numerous and extensive as were those of 1912, similarly occurred after strong winds mainly from the south and west. The Daily Weather Report shows that in the region about Scilly there was nearly a fortnight of mainly strong west to south winds preceding the stranding at Looe on 10 February. A period of mainly variable south-east to north-east winds followed until the last two days of the month when the wind was light and northerly. On 2 March strong westerly winds set in and were blowing on most days until the strandings at Bigbury on 23 March. Between that date and 2 April (the last date given in Orton's unpublished data for strandings in Plymouth Sound) the wind was often strong but variable in direction, often easterly or from the south or the north-west. Easterly and northerly winds continued for some days.

The 1934 records are for the short period from 30 October to 12 November. The Daily Weather Report shows that at the Scilly Isles strong south to west winds (Beaufort Scale 4–7) were blowing from 20 to 27 October after which the winds went to the west to north quadrant immediately preceding the first stranding at Perranporth on 30 October and remained there until 2 November when they shifted towards the south. On 4 and 5 November the wind was blowing strongly from the north-east and thereafter varied mainly between north and west until the final stranding on 12 November which was followed by a period when strong to light north to north-east winds predominated. *Physalia* at sea may have been blown out of the district by the change of wind, but as no special search was made for them this cannot be established. The few records available for this year arise solely from a few interested persons sending along for identification what were to them strange specimens. There may have been others of which we know nothing.

The 1935 specimens were stranded after winds from a westerly direction. The second half of September in that year was characterised by strong winds at Scilly mainly from between south-west and north-west and except for a few days these winds persisted throughout October and well into November.

The 1945–46 *strandings and the influence of the wind*

For the period in question Monthly Weather Reports have been published by His Majesty's Stationery Office which give summarized data for frequencies of wind force and direction at different stations for the British Isles; those for direction are utilized below. I am greatly indebted to the Meteorological Office of the Air Ministry for this and much other information including daily wind speed and direction for the Scilly Islands and special investigations into the origin and route of various air masses. The Meteorological Service, Dublin, have also been most helpful in supplying wind direction frequencies for Roches Point and Valentia.

The area in which strandings of *Physalia* occurred, or in which it was observed at sea, covers the western approaches to the English Channel and the St George's and Bristol Channels. Leaving aside for the time being the question of the more distant origin of the swarms of *Physalia*, and considering only what happened to them once they had arrived within that area, we can obtain a fairly good picture of the air movements which drove them to and fro therein by combining the wind direction frequencies for the seven stations St Ann's Head, Pembroke; St Athan, Glamorgan; Plymouth, Devon; The Lizard, Cornwall; St Mary's, Scilly Isles; Valentia, Co. Kerry; Roches Point, Co. Cork. For the first four stations I have utilized the data for 09.00 hr. G.M.T. as given in the Monthly Weather Report; for Scilly the wind-rose data from the Summary for the Year 1945, and for Valentia and Roches Point the data for 07.00 hr. G.M.T. sent to me from the Meteorological Service, Dublin. There are no outstanding differences between any of these stations and by combining them in this way an average direction frequency is obtained which can be relied on to represent with sufficient accuracy wind conditions throughout the area. Unfortunately, the data do not permit wind force to be combined with the average directional frequencies, but some idea of the force can be obtained from the wind roses for Scilly published in the Monthly Weather Reports, and from the daily records from the Scilly Islands considered below.

TABLE V. AVERAGE FREQUENCY OF WIND DIRECTION FROM EIGHT POINTS FOR SEVEN STATIONS TO THE NEAREST WHOLE FREQUENCY

1945	N.	N.E.	E.	S.E.	S.	S.W.	W.	N.W.	Calm
June	2	0	1	1	3	8	8	4	1
July	5	2	1	2	5	5	5	4	2
Aug.	4	3	3	3	2	4	6	3	3
Sept.	2	3	5	2	3	6	4	3	2
Oct.	1	3	7	3	4	4	4	1	4
Nov.	1	3	10	6	2	1	1	1	4
Dec.	2	1	2	4	4	5	6	5	1

Whilst in Table V it is obvious that in June south-west and west winds predominated, winds favourable to the arrival of *Physalia* from the west, and that in November easterly and unfavourable winds prevailed, a clearer picture can be obtained if all favourable winds be grouped together and considered as a whole, and all unfavourable winds grouped in a similar way. Before this can be done, however, it is necessary to consider which winds can be classed as favourable in the sense of blowing the siphonophores once in our area on to our shores, and which unfavourable in that they will blow them back into the open ocean. A map shows that the Scilly Islands are directly exposed to the Atlantic over an arc extending approximately from the south to the north-west. Winds from all points embraced by this arc can therefore be expected to favour the stranding of *Physalia* on our shores once other conditions farther out in the Atlantic have brought them as far east as about 10° W. and north to about 48° N. Thus of the eight-point groupings, south, south-west, west and north-west winds can be considered as being favourable, especially the last three so far as strandings on the north coast of the Devon and Cornwall peninsula are concerned. On the other hand, the north, north-east, east and south-east winds are unfavourable, they blow floating objects away and towards the open sea, though the north wind would favour the stranding on the north coast of Devon and Cornwall of *Physalia* which happened to be in the Bristol Channel, and therefore, rather like the south wind is somewhat neutral in its effect. Table VI shows the eight-point wind frequencies from all seven stations grouped and averaged to the nearest whole frequency in this manner. They have been calculated directly from the original data and not compiled from Table V which is itself an average.

From Table VI it is clear that in June the winds were almost wholly favourable on 20 out of 30 days, blowing from between the south-west and north-west. The Monthly Weather Report for June 1945 states that 'southerly and westerly winds were frequent and the month was windier than usual on the whole in England'. In July 14 days were wholly favourable as against 5 days unfavourable. There were 5 days of winds from the south and 5 days from the north; as will be shown later the north winds were mainly confined to the last week of the month so that the first 3 weeks of July continued the favourable weather of June and the winds from the south to the north-west were often strong during that period.

Table VI. Average Wind Direction Frequencies from eight points at 09.00 hr. G.M.T. grouped into favourable and unfavourable winds for Stranding on the assumption that *Physalia* travels directly before the wind

	Favourable				Unfavourable		
1945	S.W., W. and N.W.	S.	Total	Calm	N.E., E. and S.E.	N.	Total
June	20	3	23	1	3	2	5
July	14	5	19	2	5	5	10
Aug.	13	2	15	3	9	4	13
Sept.	13	3	16	2	9	2	11
Oct.	10	4	14	4	13	1	14
Nov.	4	2	6	4	19	1	20
Dec.	16	4	20	1	8	2	10

In August the winds continued on the whole to be favourable although there were more occasions on which the wind would tend to move the *Physalia* out to sea. Probably to this is to be attributed the slackening of arrivals during that month. The Monthly Weather Report for August 1945 states that 'the month was less windy than usual. Winds from between north and east were more frequent than the average'.

September showed a somewhat similar balance of favourable and unfavourable winds to that of August, though the daily records reveal that the unfavourable winds were confined mainly to the first 9 days of the month and that thereafter westerly weather with strong winds was frequent and could well account for the abundant strandings during the latter half of the month.

In October there were relatively few strandings and we note that winds from north-east to south-east were more frequent than south-west to north-west winds. In November unfavourable winds greatly predominated; there are no records of strandings for this month. December saw a reversal of these conditions and associated with this some *Physalia* were driven back again and there is one record of strandings for late December and two for the first half of January.

So far we have assumed that *Physalia* sails more or less directly before the wind and that the currents have relatively little effect on its directional movements. It is almost certainly true that ordinary slow currents have less effect on the distribution of *Physalia* than have winds of moderate strength and that for present purposes they can be ignored. We cannot, however, ignore the fact that *Physalia* most probably travels at an angle to the wind. On this point the only definite evidence is that of Woodcock (1944) who states that in the northern hemisphere *Physalia* 'is so orientated physically that it is consistently driven by the wind about forty-five degrees to the left of the direction in which the wind is blowing'. The few specimens which I had and which were well enough preserved to show the typical asymmetry of the crest agreed fairly well with Woodcock's figure for northern hemisphere animals (compare my photograph in Plate II with his fig. 46 left-hand side) and we may therefore accept as a working hypothesis his contention that movement will always be to the left of the wind direction in the northern hemisphere and to the extent of about 45°. Perhaps the extent of the deviation varies with wind strength, a fair breeze giving the full 45° to the left, a storm tending to drive the siphonophore more directly before it. Accepting, however, 45° we can regroup the wind frequencies as in Table VII. West to north winds are now the favourable ones with east to south unfavourable. North-east winds will move the siphonophore in a southward direction and are on the whole unfavourable, whilst south-west winds move it north and favour its appearance in the sea area under consideration.

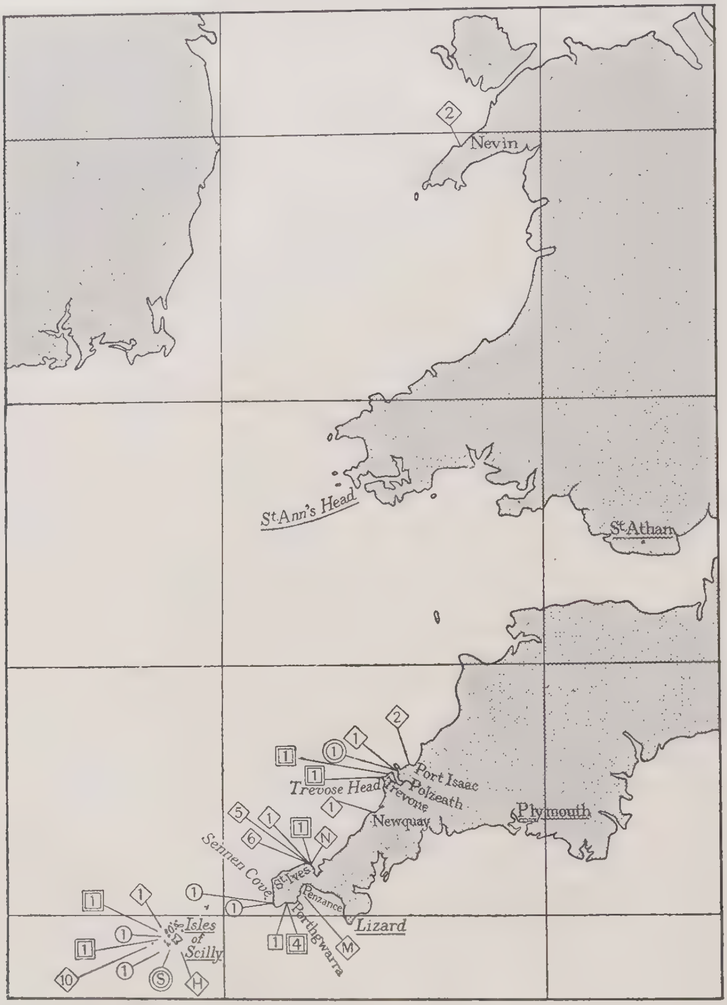
TABLE VII. AVERAGE WIND DIRECTION FREQUENCIES FROM EIGHT POINTS AT 09.00 HR. G.M.T. GROUPED INTO FAVOURABLE AND UNFAVOURABLE WINDS FOR STRANDING ON THE ASSUMPTION THAT *PHYSALIA* MOVES IN A DIRECTION AT 45° TO THE LEFT OF THAT OF THE WIND

	Favourable				Unfavourable		
1945	W., N.W. and N.	S.W.	Total	Calm	E., S.E. and S.	N.E.	Total
June	14	8	22	1	6	0	6
July	14	5	19	2	7	2	9
Aug.	14	4	18	3	8	3	11
Sept.	9	6	15	2	10	3	13
Oct.	7	4	11	4	13	3	16
Nov.	4	1	5	4	17	3	20
Dec.	13	5	18	1	10	1	11

It will be seen that grouping in this way makes little difference to the conclusions already reached on the basis that *Physalia* travels directly before the wind. Favouring winds in June are not quite so strongly marked as before but still greatly preponderate. July is hardly affected, whilst August becomes a little more favourable. September is a little less favourable than before but, as we have already seen, the unfavourable winds are mainly confined to the beginning of the month. October is more unfavourable than before and there were few strandings that month. November is as markedly unfavourable as before and again conditions are reversed in December, though not quite so noticeably. Thus for the main purpose of this investigation it matters little whether *Physalia* moves directly down wind or at some angle to the left. If a similar table be constructed on the assumption that the siphonophore would move at 45° to the right a very similar set of figures is obtained and the main conclusions as to the favourability of any particular month are unaffected.

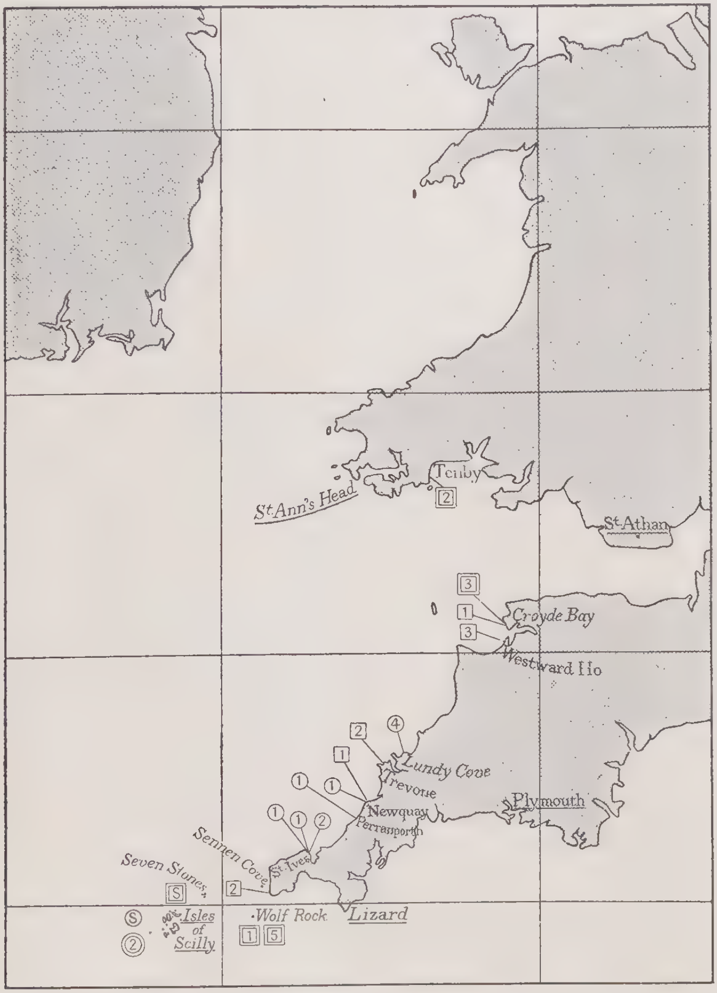
The dates of the actual strandings are known to within a day or two and have already been given in Table IV. They are all plotted at weekly intervals on the four charts (Text-figs. 1–4). It is instructive to compare them with the daily records of wind force and direction, for otherwise it is difficult to understand how apparently southerly and south-westerly winds would drive the organisms ashore on the north coast of Devon and Cornwall. For this purpose the Meteorological Office of the Air Ministry supplied me with the mean hourly wind speed and direction for the hour ending 09.00 hr. G.M.T. at Scilly. These figures should be fairly representative for the south-western area as a whole, although naturally the farther away the strandings are the less accurate are any conclusions based on them.

The first arrivals were noted at the Scilly Islands and at Sennen Cove at the extreme south-west tip of the Cornish peninsula during the first week of July. During the preceding May 'southerly and south-westerly winds were rather more prevalent than usual' (Monthly Weather Report for May 1945), whilst June had been a month of strong south-west to north-west winds with few winds from other directions. The last few days of June and the first week of July had strong winds from these directions, and it was these winds that brought in the first specimens to reach our shores. On 14 July the first *Physalia* recorded on the north coast of Cornwall was stranded at Polzeath; on that day there was a moderate breeze (Beaufort Scale 4) from the south-west, but the day before there had been a similar breeze of Scale 4 from the north-east, and it may have been this wind that brought inshore a specimen which had been travelling up the Bristol Channel. The Trevone specimen of 24 July came ashore on a light north-west wind and the north Cornish ones of 28–31 July were found when the wind was from the north. The other records for this period are for the Scilly Islands and the extreme south-west tip of Cornwall. The strandings at Penzance on 31 July do not fit quite so well into the picture and can only be ascribed to local conditions. The records of large numbers near Scilly for the end of July and the first week of August might just possibly be for specimens which had in mid-July been blown up the St George's Channel and were then travelling back before the northerly winds which were blowing from about 26 July to 9 August. Colour is lent to this suggestion by a record for Nevin on the Lleyn Peninsula, Carnarvonshire, for the beginning of August. This is an observation by a zoology student at Bangor University College passed on to me by Professor F. W. Rogers Brambell


2
Nevin
St Ann's Head
St Athan
2
1
1
1
1
Port Isaac
Polzeath
Trevone
Trevose Head
1
Newquay
Plymouth
5
1
1
N
6
Sennen Cove
St Ives
Penzance
Porthgwarra
Lizard
1
1
1
1
1
4
M
1
1
1
Isles of Scilly
10
1
S
H

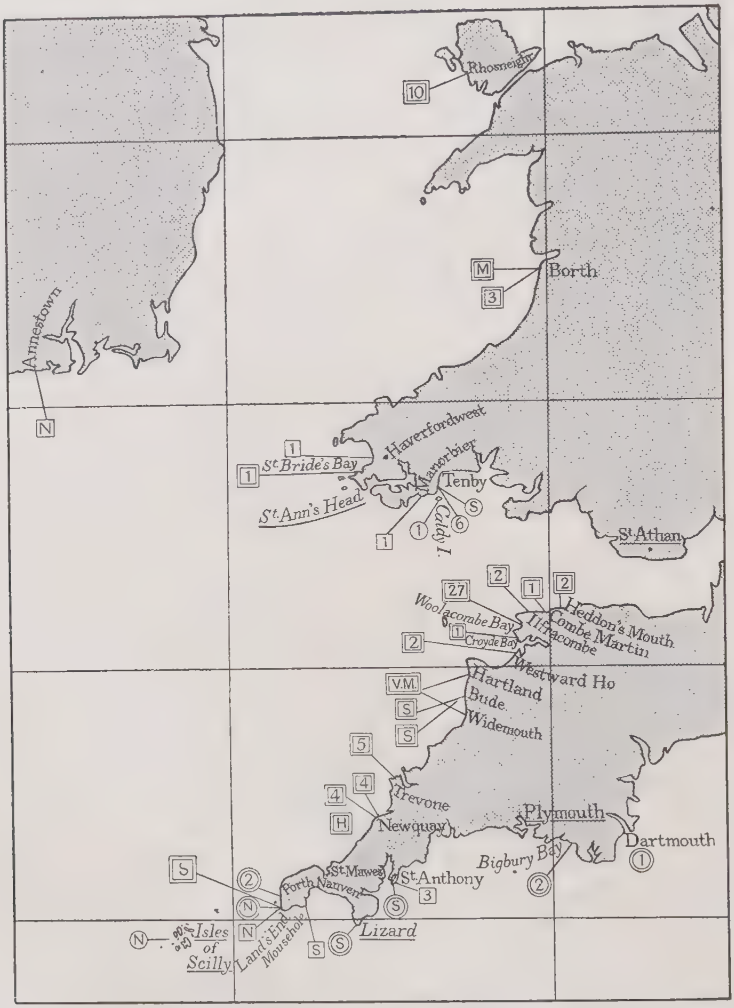
Text-fig. 1. Distribution of *Physalia* in July. ○ 1–7 July; ◎ 8–14 July; □ 15–21 July; ⊡ 22–28 July; ◇ 29 July–4 Aug. Figures and letters indicate number seen. H, hundreds; M, many; N, a number; S, several. Meteorological stations underlined.

who is convinced, after careful questioning, that the student had indeed seen *Physalia* stranded there at that time. If we accept this observation it does add to the supposition that a shoal of *Physalia* was blown towards the Welsh coasts by the strong south and south-west winds of mid-July. However, we must not lose sight of Woodcock's statement that *Physalia* travels to the left of the wind in which case a north wind would blow the organisms in a south-easterly direction and the large number seen at the Scilly Islands in late July and early August could then have come direct from the Atlantic by skirting the


St Ann's Head
Tenby
2
St Athan
3
1
Croyde Bay
3
Westward Ho
2
4
1
Lundy Cove
Trevone
1
1
Newquay
Perranporth
1
1
2
Plymouth
Sennen Cove
St Ives
Seven Stones
S
2
S
2
Isles of Scilly
Wolf Rock
Lizard
1
5

Text-fig. 2. Distribution of *Physalia* in August. ○ 5–11 Aug.; ◎ 12–18 Aug.; □ 19–25 Aug.; ⧈ 26 Aug.–1 Sept. Figures and letters indicate number seen. S, several. Meteorological stations underlined.

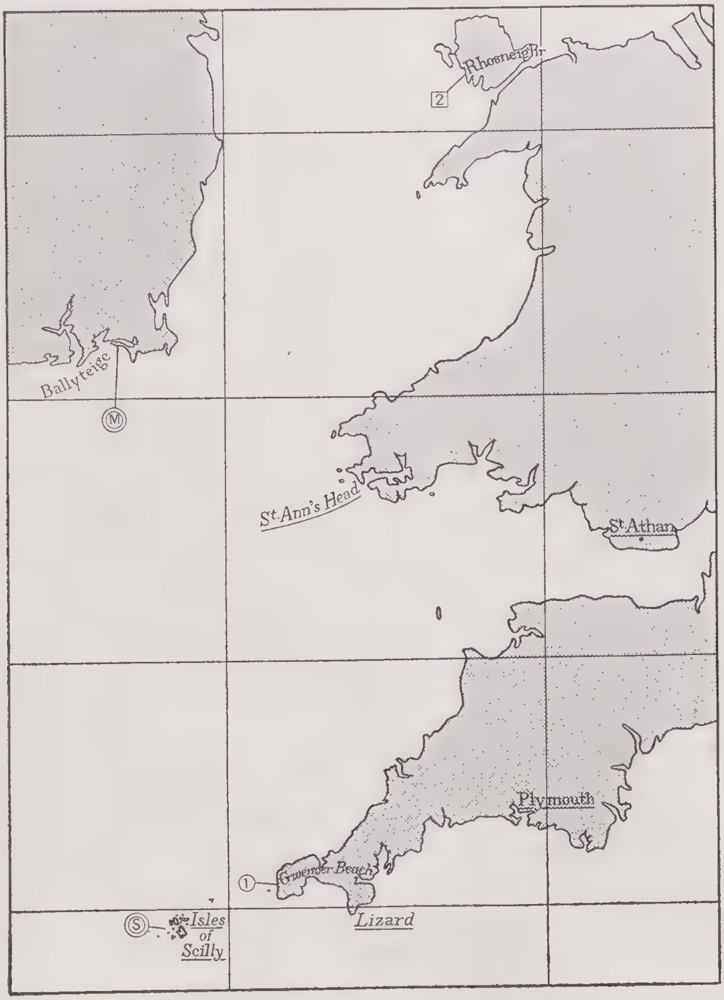
southern shores of Eire. There is always the possibility that the Nevin specimens came through the North Channel though this seems most unlikely in the absence of records farther north. Perhaps a few specimens were carried up the St George's Channel in mid-July, the vanguard of the main shoal which came in from the Atlantic later.


Rhosneigr
10
M
Borth
3
Annestown
N
1
1
St Bride's Bay
Haverfordwest
Manorbier
Tenby
St Ann's Head
S
6
1
1
Caldy I.
St Athan
2
27
1
2
Woolacombe Bay
1
Croyde Bay
2
Ilfracombe
Heddon's Mouth
Combe Martin
Westward Ho
V.M.
Hartland
S
Bude
S
Widemouth
5
4
4
Trevone
H
Newquay
Plymouth
Dartmouth
1
Bigbury Bay
2
S
2
N
Porth Nanven
St Mawes
St Anthony
3
S
N
Isles of Scilly
N
Land's End
Mousehole
S
S
Lizard

Text-fig. 3. Distribution of *Physalia* in September. ○ 2–8 Sept.; ◎ 9–15 Sept.; □ 16–22 Sept.; ⊡ 23–30 Sept. Figures and letters indicate number seen. H, hundreds; M, many; N, a number; S, several; VM, very many. Meteorological stations underlined.

There are a number of records for 5–7 August, generally of single specimens, on the north coast of Cornwall west of Lundy Cove, Portquin Bay to St Ives.

The wind was mainly from the north and the north-west during this period. Apart from the single observation of two at Scilly on 13 August no more were reported until 20 August. There was a spell of easterly winds (Beaufort Scale 3–5) from 11–14 August which doubtless accounts for the scarcity of records during the middle of the month. Moderate westerly to southerly winds then set in for 3 days after which the wind shifted again to the north and another two specimens were recorded at Trevone on 20 August. On that day a westerly wind was blowing which freshened to a north-west to west gale


Rhosneigr
2
Ballyteige
M
St. Ann's Head
St. Athan
Plymouth
1
Gwenver Beach
S
Isles of Scilly
Lizard

Text-fig. 4. Distribution of *Physalia* in October. ○ 4 Oct.; ◎ Mid to late Oct.; □ 31 Oct. Figures and letters indicate number seen. M, many; S, several. Meteorological stations underlined.

on 21 and 22 August and was still blowing strongly from the west and south-west from 23–25 August. Further strandings took place in north Cornwall and for the first time in north Devon at Croyde Bay and Westward Ho on 25 August. For the rest of the month the winds varied mainly between the east and south and were followed by strandings at Tenby in south Wales during the first few days of September. There are no more records of strandings on the north coast of the Devon and Cornwall peninsula until late in September.

North and east winds of moderate strength (Scale 3–4) characterized the first 9 days of September. Apart from the south Wales strandings and the sighting of a number of individuals at sea off and to the westward of the Scilly Islands, none was reported until in the second week when we had for the first time a number of observations for the south coasts of Devon and Cornwall as far east as at sea off Dartmouth. These came following a change of wind on 10 September to the south and west. The wind strength increased until in the middle of the month it was blowing strongly from the south-west. At this time numerous individuals were stranding in the Land's End district. On 17 September the wind went to the south and east, there is another record for Tenby on 18 September and records for Penzance and Falmouth about the same time. Most interesting of all for this period are the strandings at Annestown, Co. Waterford in Eire following strong south-east to south-west winds (Walker, 1946). These strandings occurred between 19 and 23 September when the wind there veered to the north and no more were seen. A disturbed period of strong west to north winds reaching gale force locally occurred from about 21 to 25 September and these resulted in the most numerous and most widespread strandings so far reported. They occurred principally on the north coasts of Devon and Cornwall and on the coasts of west Wales from Pembrokeshire to Anglesey and the quieter weather which followed the storms, with light winds from between west and north, still brought many ashore until the end of the month.

On the last day of September the light wind went to the east and stayed there well into October. Only near Land's End and the Scilly Islands were any more *Physalia* found until about the third week in October when a good number were reported from Ballyteige Burrow, Co. Wexford, Eire. The winds (at Scilly) had been from the east and were strong (up to Scale 7) from 15 to 19 October and it may have been these winds which had blown the *Physalia* remaining in the area away to the westward, stranding some of them on the coasts of Eire. Except for two seen on Anglesey on the last day of the month no more were reported until the end of the year. The easterly winds of November put an end to the visitation except for the few stragglers which came back again on the strong south-westerly winds of December and early January.

Thus by considering the strandings in relation to the wind direction we perceive, in broad outline, the manner in which the shoals of this floating siphonophore as they arrive in our area are driven to and fro by the shifts and changes of the surface air streams, scurried first one way and then another until eventually they either perish by stranding on a lee shore, or are blown back into the ocean whence they came.

ORIGIN OF THE *PHYSALIA* SWARMS

Physalia is a normal inhabitant of the tropical and subtropical Atlantic. Chun (1897) records it as being abundant in the early months of the year at the Canary Islands and states that it is not infrequently blown into the Mediterranean. During the cruise of the *Michael Sars* in 1910 (Murray & Hjort, 1912) *Physalia* with *Velella* was frequently seen while steaming westward from the Canaries to the Azores and on to almost 50° W. in latitudes between 28° N. and 39° N. On the eastward passage higher than 45° N. none was seen. The normal northern limit seems to be about 40° N., but that from time to time the species comes much farther north, sometimes in swarms, is already obvious. Why should this be?

The ready answer to this question is, of course, that it is blown by the wind, that unusual meteorological conditions out in the Atlantic blow it farther towards the north-east than is usual. Unfortunately, an examination of the weather charts for the whole North Atlantic for April, May and June 1945 does not show anything out of the ordinary, except possibly that there were no marked easterly winds between the Azores, Bay of Biscay and south-west England, such as are often, but not invariably, present at that time of year. However, *Physalia* has not appeared in our waters every time easterly periods have been rare. Thus in 1943 there were no easterlies to speak of and only one week (14–21 May) in 1944. (I am much indebted to a friend, Mr B. C. V. Oddie of the Meteorological Office, for the meteorological information recorded in this paragraph.)

In a letter from the Meteorological Office I have received the information that in normal years during the months of May, June and July 'the pressure gradient over the Azores region is normally favourable for winds from between W.N.W. and N.W., except from the 5th to the 29th of June, when the direction is between W. and W.S.W. Over the Canaries or off the coast of Portugal the direction is from between N.W. and N.E. through N.' Assuming that *Physalia* travels at 45° to the left of the direction in which the wind is blowing specimens in the Azores region would travel towards the east or north-east under the influence of these winds and then on nearing Portugal would tend to be diverted southward again. Provided that an abundance of *Physalia* happened to be present in the Azores region during May and June it would not need a very great change in the normal wind direction to carry them towards our shores. Incidentally the surface current charts (M.O. 466, 1945) for these months show that currents north of about lat. 45° N. flow predominantly in our direction whereas off the coast of Portugal and the Canaries, where the winds are also generally unfavourable, they flow in general southward. It seems more probable therefore that the source of an invasion of these waters by *Physalia* is somewhere in the mid-Atlantic Azores region rather than in the region of the Canaries to Gibraltar. The latter cannot, however, be entirely ruled out.

The Meteorological Office has kindly examined the pressure distributions for occasions when the air arriving off the south-west of the British Isles could be traced back more or less directly, (*a*) to the mid-Atlantic Azores region, and (*b*) to the area contained by the Azores, Lisbon and the Canaries. There were three occasions in June and six occasions in July when air originated from north to north-west of the Azores (mainly south of lat. 45° N. and west of long. 20° W.). The time taken by the air to cover this distance varied from about 1½ to 3 days and it is not conceivable that the *Physalia* themselves travelled at that rate though the resultant effect of the air stream would, in the absence of easterlies, have been to push them along in our direction. Air from the Azores, Lisbon, Canaries triangle arrived in June on several occasions during the first 10 days (a period when air also arrived from the Azores district) and during two short periods in July. I feel, however, that these data are too inadequate for conclusions to be based on them.

At the moment it seems impossible to trace these occasional visitations right back to their source. They originate possibly in the first instance through the production of an unusual abundance of individuals brought about by conditions exceptionally favourable for development of the eggs and young. This might take place well to the south and should it coincide with meteorological conditions that drive many farther north than usual, and should they then be caught up in streams of air flowing strongly towards the north-east they will eventually reach the south-westward approaches to these islands, where they will then be driven hither and thither by our local winds as has been shown in the preceding section.

Associated Organisms

A number of other Atlantic organisms came ashore with the *Physalia*. The records for these are not at all complete and can only be regarded as an indication of what might have been found had the whole of the north Cornish coast in particular been under observation by competent naturalists.

Lepas fascicularis and *L. pectinata*

On 30 September 1945 the Director of this Laboratory, Mr F. S. Russell, found stranded on the Fistral beach at Newquay, along with *Physalia*, several living specimens of the floating barnacle, *Lepas fascicularis* Ellis and Solander, and brought back a number to Plymouth. They varied in size from quite small to specimens with capitula 4 cm. long. They were generally attached to floating strands of *Fucus*, but the larger groups were mainly buoyed up by their gas-bubble floats. With them were a few *Lepas pectinata* Spengler.

L. fascicularis has been recorded from time to time before; thus Orton & Rawlinson (1934) report it (with *L. pectinata*) from Trevone, near Padstow, in August 1933 and Professor Orton, in a private letter, tells me that he had it again in September 1944 at the same place. Mr O. D. Hunt (unpublished record) had one specimen, to which were attached three individuals of *L. pectinata* Spengler in the mouth of the River Yealm, S. Devon, in September 1934, the same month and year as Orton & Rawlinson's record. In the museum of the Laboratory there are two small specimens of *L. fascicularis* which were found with *L. anatifera* drifting in Wembury Bay, near Plymouth, in June 1937, and a few *L. pectinata* from a floating buoy in November 1935.

Perhaps both these species would be found in the south-west more frequently than is at present realized were it possible for competent naturalists to keep a constant watch for them along the whole of the coast-line. As it is, Orton & Rawlinson found only seven or eight records of the appearance of *L. fascicularis* 'on the south coasts of England and the same number for the west and north of Ireland'. They also state that '*L. pectinata* has been recorded only about five times since 1803 from the coasts of the British Isles'. Their paper should be consulted for the references. It has been stated (see Murray & Hjort, 1912) that *L. fascicularis* regularly invades the northern North Sea through the Faroe-Shetland channel along with other oceanic forms from the Atlantic and that immense swarms of it are to be found there in May and June.

Velella

Along with the *Lepas fascicularis* and the *Physalia* Mr Russell also found many *Velella* skeletons; there were no living *Velella*. Miss Walker (1946) also found one *Velella* float with the many *Physalia* near Tramore in late September 1945. Professor F. W. Rogers Brambell also informs me that he identified a living specimen of *Velella* which was picked up at Llanbeddr, Merioneth, on 11 June 1945 and that on 21 June numerous floats, denuded of tissue, were found among the flotsam at high-water mark in Malltraeth Bay, Anglesey. These are the only records I have been able to collect for 1945; it seems most unlikely that had many living *Velella* been stranded at the same time as the *Physalia* their bright colours would not have attracted attention and specimens been sent to this Laboratory along with its larger relative. There is not the slightest hint in any of the correspondence that *Velella* was also stranded at the same time and it seems reasonable to conclude that only a relatively few living specimens at most could have been present along with the *Physalia*.

I do not propose to discuss past *Velella* records here. They are much more numerous than are those for *Physalia*. Unfortunately it is not always clear whether the records refer to living specimens or only to the skeletons of the floats which survive for a long time after the death of the living tissues. Future recorders would do well to be clear on this point.

Turtles

Three young Loggerhead Turtles, *Caretta caretta* (L.), were sent alive to the Laboratory in August 1945. They are listed below (Table VIII).

There is no doubt that they were true *Caretta caretta* (L.) and not *Colpochelys kempi* Garman (see Deraniyagala, 1939). No. 1 had some growths of living hydroids on the plastron and neck. They seemed to agree with *Clytia johnstoni* (Alder) and *Obelia geniculata* (L.). No. 2 was clean, probably because although found on 10 August it was 24 August before we actually received it. No. 3 had some hydroids on the paddles: apparently *Obelia geniculata* (L.) and a *Gonothyrea* sp. It was stated to have had a cluster of ship's barnacles (*Lepas*) several inches long attached to the plastron; unfortunately they had been removed and were not seen by us. On the carapace were tufts of an alga identified as the American *Ectocarpus Mitchellae* Harv. (see Appendix, p. 171). A photograph of this turtle appears in illustration of an article by Parker (1946).

TABLE VIII. LOGGERHEAD TURTLES FROM NORTH CORNWALL, AUGUST 1945

Specimen no.	Date	Locality	Carapace Max. length (cm.)	Carapace Max. width (cm.)	Finder
1	7. viii. 45	In the sea off Hayle	18·5	16·5	Mr S. J. Thomas
2	10. viii. 45	Ashore on Gwithian Sands, Hayle	20·0	16·5	Master Richard Buckner
3	25. viii. 45	Ashore on Crooklets Beach, Bude	20·0	18·0	Mr A. E. Jewell

Stendall (1945) records a specimen of *Caretta caretta* with a carapace 13 in. long found swimming in the River Bann near Castlerock, Co. Londonderry, on 8 August 1945. Freeman (1946) records two small specimens of the same species washed ashore on Sherkin Island, Co. Cork, during a storm in late December 1945. One seen had a carapace 7½ in. long; the other was of about the same size. Mr H. W. Parker of the British Museum (Natural History) informs me that he received three specimens of *C. caretta* stranded as follows:

(1) Collister Beach, west side of Unst, Shetland, 13 December 1945.
(2) Oxwich Beach, Glamorgan, 7 February 1946.
(3) North Uist (west side), Hebrides, 13 February 1946.

Records of strandings of Loggerhead Turtles are fairly frequent in the literature (e.g. Parker, 1939) but in view of the findings of Deraniyagala (see his 1939 paper for references) some of the earlier identifications may have confused the species and some of the Loggerheads previously recorded may have been Kemp's or Ridley's Loggerhead which breeds only, so far as is known for certain, on the American side. The Loggerhead occurs, of course, on both sides of the tropical and subtropical Atlantic but in a recent popular article Parker (1946) discusses the occurrences of both species of turtle on our coasts and inclines to the opinion that they may possibly originate in the Caribbean whence they are started on their journey across the Atlantic by violent local storms. If this be so—the idea is now strengthened by the occurrence of the American *Ectocarpus* in one of the turtles mentioned above—then the turtles stranded with the *Physalia* in 1945, and possibly also those stranded in early 1946, may have been half-way across perhaps near the Azores region in the spring or summer of 1945. They would there be caught up by the same conditions that favoured the passage to our shores of the shoals of *Physalia*, for like the latter, they are surface organisms and, for much of the time at any rate, expose considerable areas of their bodies above the surface of the water.

Lampris luna

One other possibly associated occurrence should be mentioned. This was the capture in Bigbury Bay, S. Devon, on 2 August 1945 of a Moon-fish or Opah, *Lampris luna* (Gmelin). It was taken by holiday-makers whilst struggling, half-stranded, in shallow water, on a falling tide. It was a male over 3 ft. long and weighed 60 lb. The stomach and intestines were opened by Miss Nora G. Sproston; she found the beaks of forty-one cuttlefishes which appeared to have been eaten quite recently and, in addition, the recognizable remains of four sand-eels, two pilchards and other organisms not possible to identify.

Norman & Fraser (1937) state that *L. luna* is widely distributed in the warmer parts of the Atlantic and that it is 'a not infrequent visitor to the coasts of the British Isles during the warmer months'. They go on to say that 'it probably spends a good deal of its time close to the surface, but there is no doubt that at times it descends into deeper water'. If the Bigbury specimen had been spending much of its time at the surface it is just possible that it too had come under the influence of winds and surface drift that favoured its passage towards our south-west coast. On the other hand, it is equally likely that its appearance at the same time as the *Physalia* and turtles was pure coincidence.

General Considerations

The occurrence of a number of other organisms from the warmer parts of the Atlantic along with the swarms of *Physalia* in 1945 might be held to indicate a drift of Atlantic water into the approaches to the Channel. The organisms in question, however, should, on the whole, be regarded as wind-borne types rather than water-borne and it does not seem reasonable to consider them as reliable indicators of water movements in the way that some wholly submerged plankton organisms can be so regarded. Unfortunately, owing to the lack of a suitable vessel it was not possible at the time to make a proper search for any such indications at sea.

Stephen (1938), Russell (1939) and others have referred to the northward spread during the 1930's of warm-water organisms in the North Atlantic corresponding to a rise in temperature of the northern surface waters of that ocean and its branches such as the North Sea. Such a rise, if maintained, might well be a factor in assisting the penetration northward of an organism such as *Physalia*, enabling it perhaps to breed in latitudes higher than is usual, perhaps thus favouring the formation of shoals of the adult in a region whence the winds blow mainly towards our shores. However, Dunbar's recent investigations (1946) into the temperature records for the west Greenland current have shown that whereas a warm period appears to have reached its peak in the middle of the 1930's, more recent years, particularly 1942–4 have shown a cooling due to a weakening of the Atlantic influence. If this return to colder conditions be general for the North Atlantic, *Physalia* and the other organisms penetrated northward in 1945 in spite of rather less favourable temperatures than had perhaps aided their predecessors in 1934. The facts, indeed, once again point to the wind as being the main factor responsible for these occasional visitations of animals from southern regions, water movements playing only a minor role in their distribution.

THE CAPTURE AND DIGESTION OF PREY

Historical

The virulence of *Physalia* stings and the strange manner of digestion of its relatively large prey have often been described and yet, as Gudger (1942) truly remarks, 'only a few students of marine life have seen *Physalia* catch and eat fishes, and their accounts are widely scattered in scientific books and journals'. He does a real service by gathering together the few such accounts of any importance which are available, and he gives a number of references not quoted here. According to him the earliest first-hand recorded observation of the fish-eating activities of *Physalia* is by Quoy & Gaimard (1824). Bennett (1837) describes the *tentacula* as 'capable of being coiled up within half an inch of the bladder and then darted out with astonishing rapidity to the distance of 12 or 18 feet'. Food seized by them is rapidly conveyed to the mouths. Years later Bennett (1860) gave a short but graphic description of the seizure and digestion of little fishes. Lesson (1843) often saw small *Physalia* kill fish as strong as a herring and stated that flying-fishes are its principal food. He briefly describes the absorption of the products of digestion by the siphons. De Quatrefages (1854) saw a dead fish, 8–10 cm. long, held by a *Physalia*. It was surrounded by thick mucilaginous matter and in about an hour was almost entirely dissolved. A large siphon had partially engulfed the tail. With a lens he followed the digested matter passing up the siphons. Collingwood (1867) and Wallich (1869) both have interesting observations on *Physalia* seen at sea. The former gives a graphic account of the effect of the stings on a seaman and mentions having seen an albacore swallow a *Physalia* and its accompanying shoal of commensal fishes (*Naucrates*). Wallich wound off the tentacles 'in the same way that one may wind off a skein of silk', stretching them from 3 to 6 in. to 8 or 10 yards. Mortimer (1877) also has observations on the stinging properties of the tentacles and their contractility. Bigelow (1891) gives a fairly detailed account of experiments with living *Physalia* at Woods Hole in July and August 1889 when the organism was abundant in Vineyard Sound and he was able to keep a number of specimens alive in the tanks for a week or more. He well describes the capture of small fishes and their subsequent digestion by the siphons and he gives a rough sketch of the manner in which the latter attach themselves to the prey. This is the only figure I have been able to find which shows this remarkable feature of the alimentary system. Mercier (1924) reported some effects of the stings on human beings. Parker (1928) gives a popular account of the habits of *Physalia* stating that 'it is not unusual to find...the remains of several partly digested fishes still held to the underside of the float. Sooner or later these are cast off.' In 1932 the same author gave a detailed description of the structure of the dactylozooids and showed that their rhythmic contractions are neuromuscular in nature. He stated that they may reach a length of over 9 m. and shorten to one-seventieth of their maximum length. Richet & Portier (1936) describe experiments, performed on frogs and other animals, of the toxicity of the poisons injected by the nematocysts and discuss the phenomenon of anaphylaxis.

Few photographs of living *Physalia* appear to exist. Bouxin (1936) reproduces photographs of two battered pneumatophores from which most of the polypoid persons were missing. Woodcock (1944) gives a figure from a photograph of what seems to have been a recently killed specimen. Buchsbaum (1938) has a fine photograph supplied by the New York Zoological Society, of a specimen eating a small fish. In a private letter to me he has confirmed that the photograph was from life. Unfortunately, only the tail-end of the fish can be seen and the detail of the manner in which it is held is not clear. Photographs of a model appear in Parker (1928), Gudger (1942) and elsewhere.

OBSERVATIONS AT PLYMOUTH

The living *Physalia* which was received on 3 August 1945 and which had been taken from the sea in the neighbourhood of the Scilly Islands and forwarded to Plymouth by Major A. A. Dorrien Smith enabled me to make a number of observations on feeding and other habits. Most of these confirm earlier writers, whose papers incidentally I did not see until after my notes had been made.

The *Physalia* reached the Laboratory on the evening of 3 August. It was in a large Kilner jar partly filled with sea water and was in fresh condition although its movements were few and slow. It was immediately placed in a clean tank arranged for photography and some records were taken of it at once. The pneumatophore was at this time sausage-shaped with an overall length of about 9 in. (23 cm.) and with the crest a crumpled ridge along the top. The dactylozooids all hung down to the bottom of the tank, for a time almost motionless. The *Physalia* gradually increased its activities, rolling the pneumatophore from side to side, and the dactylozooids began to show rather irregular elongations and contractions. In this condition it was left for the night, a board being placed as a cover over the tank. On raising the board the following morning it was seen that the crest was depressed as on the previous evening, but on splashing sea water over the pneumatophore the crest slowly rose. Whether this was due to the drops of water simulating sea spray, or whether the action produced a 'wind' to which the pneumatophore reacted it is not possible to say. Bigelow (1891) produced erection of the crest by blowing on it with bellows. The crest was depressed and raised two or three times more, but subsequently it remained up for most of the period the *Physalia* was still alive. With the raising of the crest the pneumatophore shortened to about 7 in. (18 cm.).

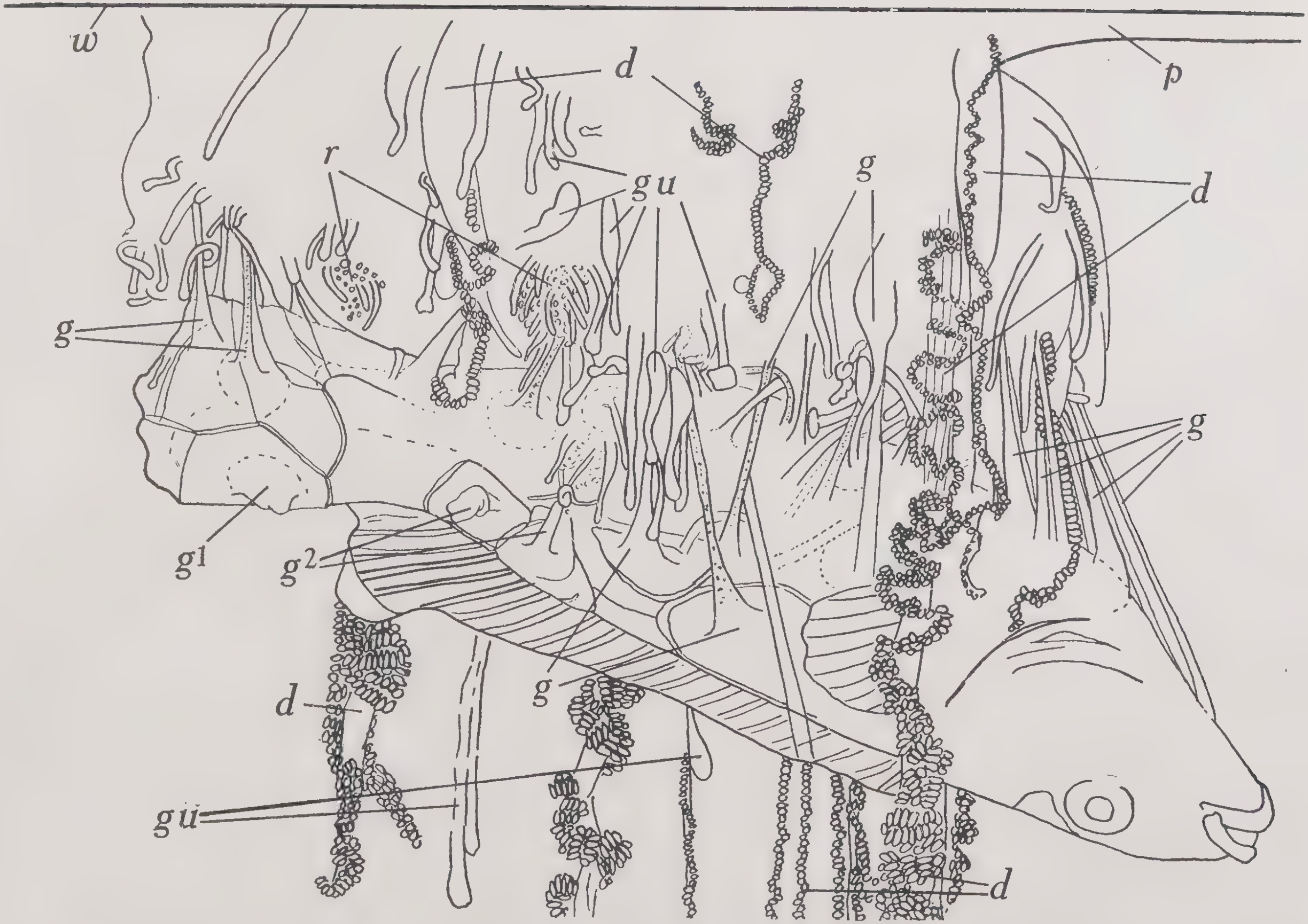
The rolling action of the pneumatophore continued from time to time, the whole thing rolling slowly over first to one side and then to the other, dipping the crest in the water. Plate II shows the pneumatophore over on its right side (regarding the free end of the pneumatophore as anterior) whilst the crest was being slowly raised again after immersion under the surface. It will be noted how the bases of some of the polypoid persons are lifted above the surface; the pneumatophore may have been the more easily able to do this by being in contact on its left side with the background sheet of ground glass. Bigelow (1891) states that his specimens always tended to lie over in this position and never on their left sides. The specimen I had generally went over alternately from side to side, especially when it was floating in a much bigger tank than that in which it was photographed. My impression was that the action was directed towards keeping the surface of the pneumatophore wet, perhaps a necessary precaution in the tropics in calm weather when no spray is flying. Wallich (1869) observed this, or an almost identical action, taking place at sea. He saw *Physalia* turning slowly over on one side as it came 'abreast of the bows of the ship, the state of depression continuing until it is abreast of the stern'. He had 'repeatedly witnessed this wonderful occurrence in moderately calm weather, at distances varying from a few feet to thirty and even fifty yards' and he was inclined to attribute it to some vibratory influence from the passage of the ship, although the depression often took place 'apparently quite beyond the reach of the surface-disturbance of the water, which causes a series of advancing waves ahead of the ship'. Specimens placed on cardboard immediately after capture continued this slow rolling movement until the wall of the pneumatophore had actually shrivelled with the heat. De Quatrefages (1854) and Huxley (1859) both refer to the somersaulting activity of the float consequent upon the raising up out of the water of the pointed end. This raising up of the pointed end was seen in the Plymouth specimen when it was blown gently across a large tank. Huxley stated that he watched the trembling action of the float 'going on with great vigour in a dead calm' when it could not be a reaction to wind. This appears to confirm my suggestion that it may, at least partly, be a wetting action.

The activity of the pneumatophore is indeed astonishing to those seeing it for the first time. Major A. A. Dorrien Smith in a letter to me relates how 'it has the power to lever itself by the cap of the gas bladder out of a bucket when the water is say, an inch or so from the top'. The crest itself is rarely static, varying its shape and height slightly the whole time whilst raised.

The colouring was vivid and of great beauty, it has often been described and my notes do not add to it in detail. It is sufficient to record that in the Plymouth specimen the float was pale blue shot with pink, the crest pink. The polyps were blue and purplish, the long dactylozooids mainly a deep dark blue. Some colour photographs were taken and may subsequently be published elsewhere. Unfortunately, the colours are not truly rendered in the photographic transparency, the pink especially not being recorded at all well.

The dactylozooids were continually elongating and contracting, some shortening as others were lengthening. They extended down to the bottom of the tank which was relatively shallow, and at times trailed a little on the bottom. The deeper the tank the more they elongated, but the deepest tank the specimen was placed in was much too shallow to allow the dactylozooids full play.

An opportunity to judge of their stinging power occurred when a small wrasse (*Ctenolabrus rupestris*), 4 in. long, inquisitively investigating, came into contact with one of them. The fish gave an immediate and violent kick which only brought it into contact with yet others; it was unable to get away. Soon several dactylozooids were festooned about the unfortunate wrasse (see Pl. I) which was hauled up by them towards the gastrozooids that extended with active squirming movements to meet it, some quickly fastening on to it. At this stage the movements of the fish were spasmodic and violent and it succeeded in breaking away from the gastrozooids for a time and from some of the dactylozooids. I am not sure that this may not have been due to partial exhaustion of oxygen in the water by the violent activities of both captor and captured. They were at the time in a restricted space in my photographic tank from which the sea-water inflow had been turned off whilst photographs were being taken. On resuming the water supply the *Physalia*, which had secreted



Text-fig. 5. Key to Pl. III. *d*, dactylozooids; *g*, gastrozooids attached to the fish; g^1, a gastrozooid whose main body passes down behind the tail and bends round to spread its lips on this side; g^2, gastrozooids broken across during the struggles of the fish; *gu*, unattached gastrozooids; *p*, pneumatophore; *r*, gonozooids; *w*, water surface.

a fair quantity of mucus, recovered from its temporary exhaustion and this time properly secured the fish, which incidentally was turned round in the process. Many gastrozooids got a firm hold and an hour after it had first been caught the wrasse died. The fishes which Bigelow fed to his *Physalia* also took an hour to die. The gastrozooids spread their lips over the wrasse until it was completely or almost completely covered by them. Pl. II shows the dead fish held by the gastrozooids only, the dactylozooids had released themselves from it and were trailing again. This photograph was taken about an hour after that in Pl. I. Pl. III shows in more detail, and with differently arranged lighting, the attachment of the gastrozooids; it was taken about half an hour after Pl. II when digestion had been proceeding for some time. A key-drawing to this photograph is provided so that the main points of interest can be referred to. In all about thirty gastrozooids can be distinguished as being definitely attached to the fish, most of them on the side facing the camera. Others are attached on the other side and are out of sight, probably in all fifty to sixty gastrozooids are fixed to it. Of these two had their stems broken across during the early struggles of the fish but still cling tightly to its back (Text-fig. 5, g^2). The stems of two or three gastrozooids pass down one side of the fish and curl round to spread their lips on the other side. An example of this is seen at g^1. The mouths spread out in trumpet-shaped fashion until the edges of the lips touch one another, or even overlap to some extent. This is most clearly seen on the tail and mid-region of the body. It was found impossible to light the subject so that all details showed with equal clarity at one and the same time, and as the fish was swinging slowly with movement imparted to it by the contractile activities of the various polyps it was not easy to foretell what the effect would be at the instant of exposure. All exposures were by foil-filled flash bulbs so that the light by which the photograph was taken was not that by which it was being observed. Thus the gastrozooids on the head region have not been picked out by the lighting as well as are those on the tail, though to the eye they showed up just as clearly. By the time the plate had been developed and examined the *Physalia* was releasing the remains of its victim so that it was not possible to obtain another picture.

The gastrozooids were very transparent and partly digested particles from the skin of the fish could be seen passing up inside them. These are visible as dark granules in a number of gastrozooids seen in the photograph (dotted in diagram, Text-fig. 5). About an hour after digestion had begun the fish was released and dropped away; much of its surface layer had been digested. Sea-water circulation to the tank was running at the time so that this action does not appear to have been the result of shortage of oxygen. Probably it is normal with a relatively large fish, only a portion being utilized for food.

The gastrozooids covered almost all the surface of the fish except possibly a portion of the dorsal fin, which in the photograph looks to be uncovered on this side. A considerable quantity of mucus is sticking to its posterior lobe.

In the photograph many unattached gastrozooids (*gu*) can be observed and two bunches of gonozooids (*r*) as well as dactylozooids (*d*) of various sizes.

The *Physalia* lived for about 5 days when it was killed with formalin and preserved. By that time it had lost most of its polyps, the gonozooids dropped off about the second day and the dactylozooids broke off, especially when they trailed to the bottom of the tank and caught up against rocks and sea-anemones. Another small *Ctenolabrus* which rushed out to bite at a fragment of tentacle, spat it out immediately and retreated under a rock with very marked discomfiture. Towards the end the pneumatophore had become very sluggish, though it kept the crest at least partly erect most of the time.

Note on the Specific Name

Recent authorities are of the opinion that there is only one cosmopolitan species of *Physalia*, an opinion with which Mr A. K. Totton of the British Museum (Natural History) tells me that he concurs. In the *Plymouth Marine Fauna* 1931 the name is given as *Physalia* (sp.?) *arethusa* (Browne). It appears that Browne's name is pre-Linnean and that the correct name is *Physalia physalis* Linnaeus.

Acknowledgements

Grateful thanks are due in the first place to all those people who took the trouble to respond to the appeals by Professor Orton and myself for specimens and details of strandings. The names of these ladies and gentlemen are recorded in Tables IV and VIII and on pp. 144–5 and 160; without their aid the first part of this paper could not have been written. A special word of thanks is due to Major A. A. Dorrien Smith for all the trouble he took in observing *Physalia* at sea and in procuring specimens, and especially for the fine living specimen on which the second part of this paper is based.

Some acknowledgements have already been made at appropriate places in the text. A number of other people assisted in various ways, by supplying me with references or copies of references to which I could not otherwise have obtained access. In this connexion Monsieur Ch. Bocquet, Roscoff; Mr P. H. T. Hartley, Oxford; Mr A. W. Stelfox, Dublin; Mr A. K. Totton, London; Prof. R. Weill, Bordeaux, and the Librarian of the London School of Hygiene and Tropical Medicine should be especially mentioned.

The Meteorological Office of the Air Ministry, Harrow, has been most helpful in supplying essential meteorological data and my friend Mr B. C. V. Oddie of the Meteorological Office of the R.A.F., Gloucester, has likewise taken considerable trouble to obtain for me information with regard to the winds over the Atlantic.

I am deeply grateful to Professor J. H. Orton for pooling the whole of his material and records with mine and for allowing me to incorporate the records he collected in 1912 and 1913. Thanks are also due to various members of the staff of this Laboratory and to its Director, Mr F. S. Russell, for their interest and assistance in various ways.

SUMMARY

The occurrence in the summer of 1945 of a swarm of *Physalia physalis* L. off the south-west coast of the British Isles has initiated a survey into records of its appearance on the Atlantic coasts of Europe during the past 100 years. Unpublished records for 1912, 1913, 1934 and 1935 were discovered and are listed with those already known. The 1945 strandings are considered in detail in conjunction with meteorological data for the period involved. It is concluded that winds, rather than water movements, are the main factor in transporting the swarms towards the British Isles and it is considered likely that the swarms come from the Azores-mid-Atlantic region rather than from the Canaries-Gibraltar district.

Associated with the *Physalia* were *Lepas fascicularis* and *L. pectinata*, some *Velella*, a few turtles (*Caretta caretta*), and possibly an Opah fish (*Lampris luna*), all of them, with some reservation respecting the last-named, surface organisms that would come under the same meteorological influences as the *Physalia*.

A living specimen of *Physalia* gave an opportunity to observe the method of feeding of which few previous first-hand accounts exist. The capture of the prey by the dactylozooids and its subsequent digestion by the gastrozooids is illustrated by photographs from life and is described in some detail. It is suggested that the rolling of the pneumatophore from side to side, dipping the crest in the water, is a calm-weather habit directed to keeping moist the upper surface exposed to the air.

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EXPLANATION OF PLATES I–III

PLATE I

Physalia physalis L. catching a *Ctenolabrus rupestris* (L.). × $\frac{3}{4}$ approx. The dactylozooids are wrapped about the fish which is still alive. Flashlight photograph from life.

PLATE II

Physalia physalis L. eating the *Ctenolabrus rupestris* (L.). × $\frac{3}{4}$ approx. Gastrozooids are attached to the dead fish whilst the dactylozooids are detached and trail freely. The pneumatophore is heeled over on one side with the crest towards the camera. Flashlight photograph from life about 1 hr. after that shown in Pl. I.

PLATE III

A close view of the gastrozooids of *Physalia* attached to the fish. × $1\frac{1}{2}$ approx. An explanatory key is given in Text-fig. 5. Flashlight photograph from life about half an hour after that shown in Pl. II.

APPENDIX

Dr M. Parke of this Laboratory and Miss C. T. Dickinson of the Kew Herbarium have kindly identified for me the *Ectocarpus* found growing on Turtle No. 3 (see p. 160), and they have supplied me with the following note:

The *Ectocarpus* species growing on the carapace of Turtle No. 3 was identified as undoubtedly a form of *E. Mitchellae* Harv. Plants bearing both unilocular sporangia and meiosporangia were present but none bearing megasporangia. The material approached most closely the variety *E. Mitchellae* Harv. var. *parvus* Taylor, but was taller and slightly more robust than the type as described by Taylor (1921, p. 254). This variety was recorded by Prof. Taylor from southern Massachusetts, growing affixed to the carapace of a marine turtle and to floating timbers, and fruiting in summer (1937, p. 112).

The material was sent to Prof. Taylor (by C.T.D.) for verification; he replied saying the material was certainly *E. Mitchellae* Harv., and if his var. *parvus* was a true variety it would apply as he thought there was no significant discrepancy in the measurements.

Although *E. Mitchellae* Harv. is now recorded by many workers as occurring in Europe, the European plant was first given the manuscript name of *E. virescens* by Thuret and was published as a *nomen nudum* only by Flahault (Thuret in Flahault, 1888). Owing to the similarity between the Atlantic-American and the European material many phycologists have classed them as one species and have therefore used Harvey's name, *E. Mitchellae* (the older name), for the European records, *E. virescens* Thur. being given as a synonym.

There still seems to be some doubt as to whether the Atlantic-American plant is identical with the European plant. Børgesen (1926, pp. 18–23) and Sauvageau (Børgesen, 1926) keep them separate. Sauvageau, who at first considered they were the same species, later decided that it would be more prudent to maintain the two species separately in spite of their close resemblance.

Geographical distribution. E. Mitchellae Harv. is recorded from: West Indies, Bahamas, Texas, Florida, Bermuda, North Carolina, Rhode Island, southern Massachusetts and Nantucket. *E. virescens* Thur. is recorded (sometimes as *E. Mitchellae* Harv.) from Great Britain to the Canary Islands.

C.T.D.
M.W.P.

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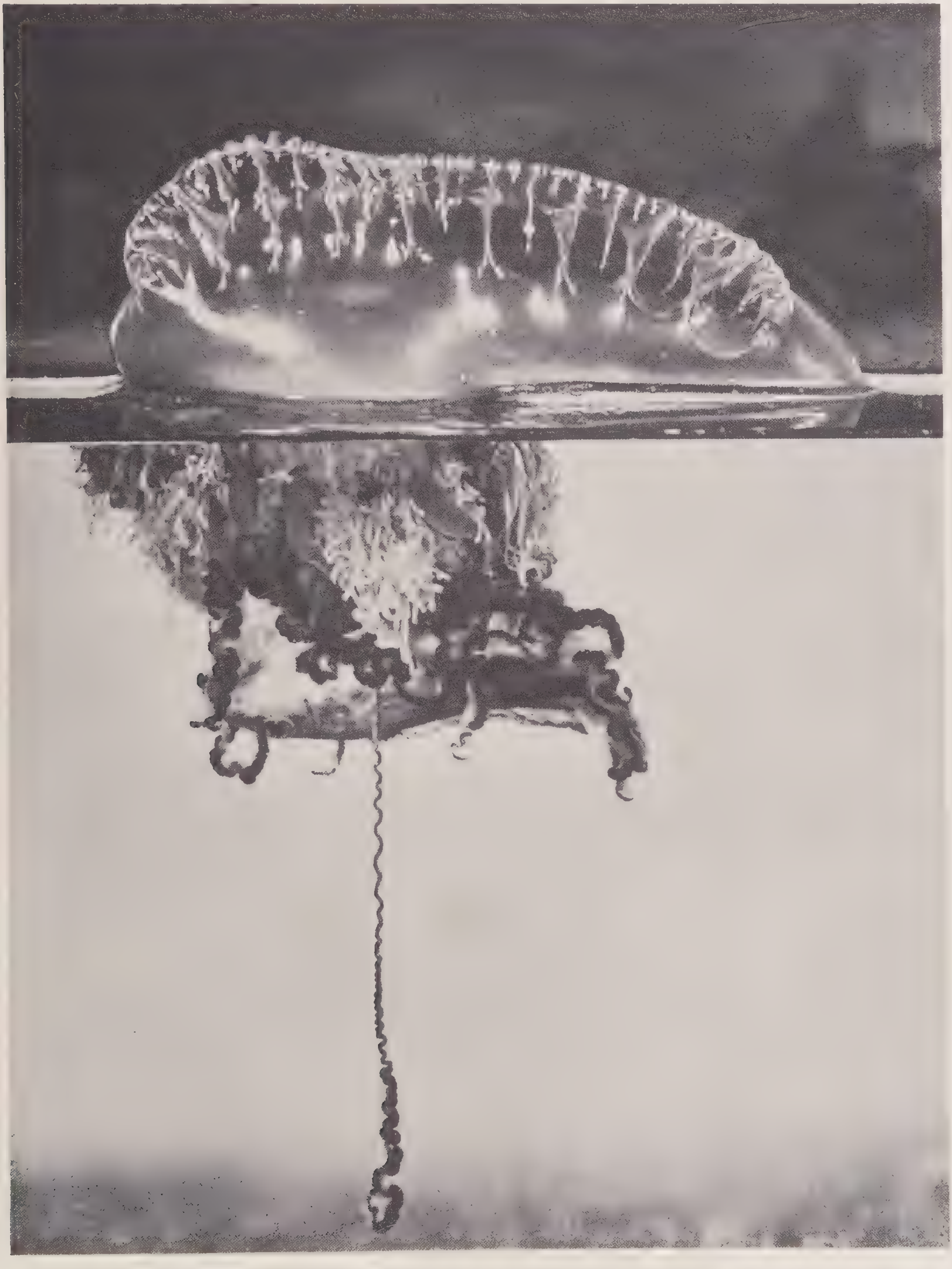
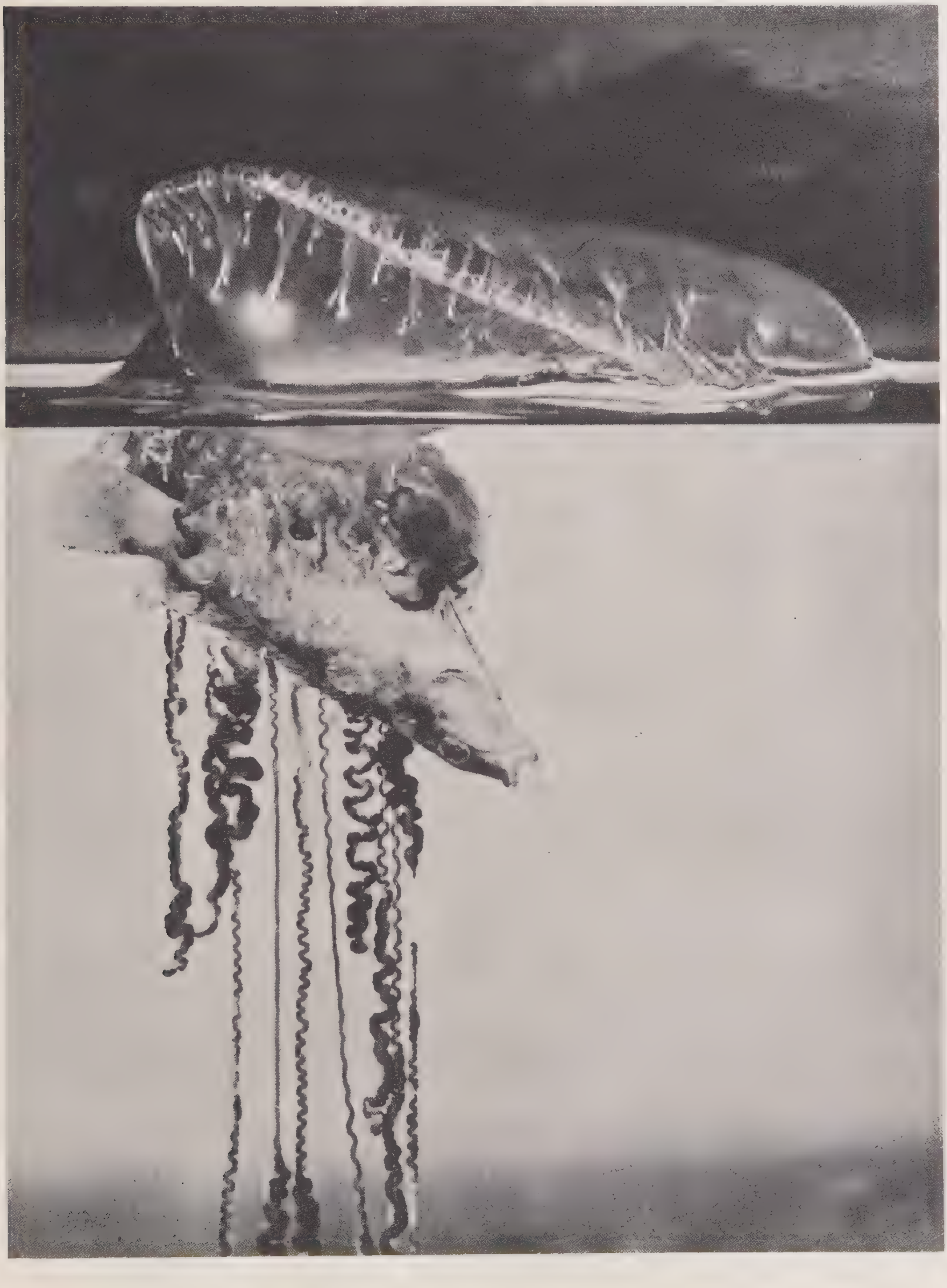
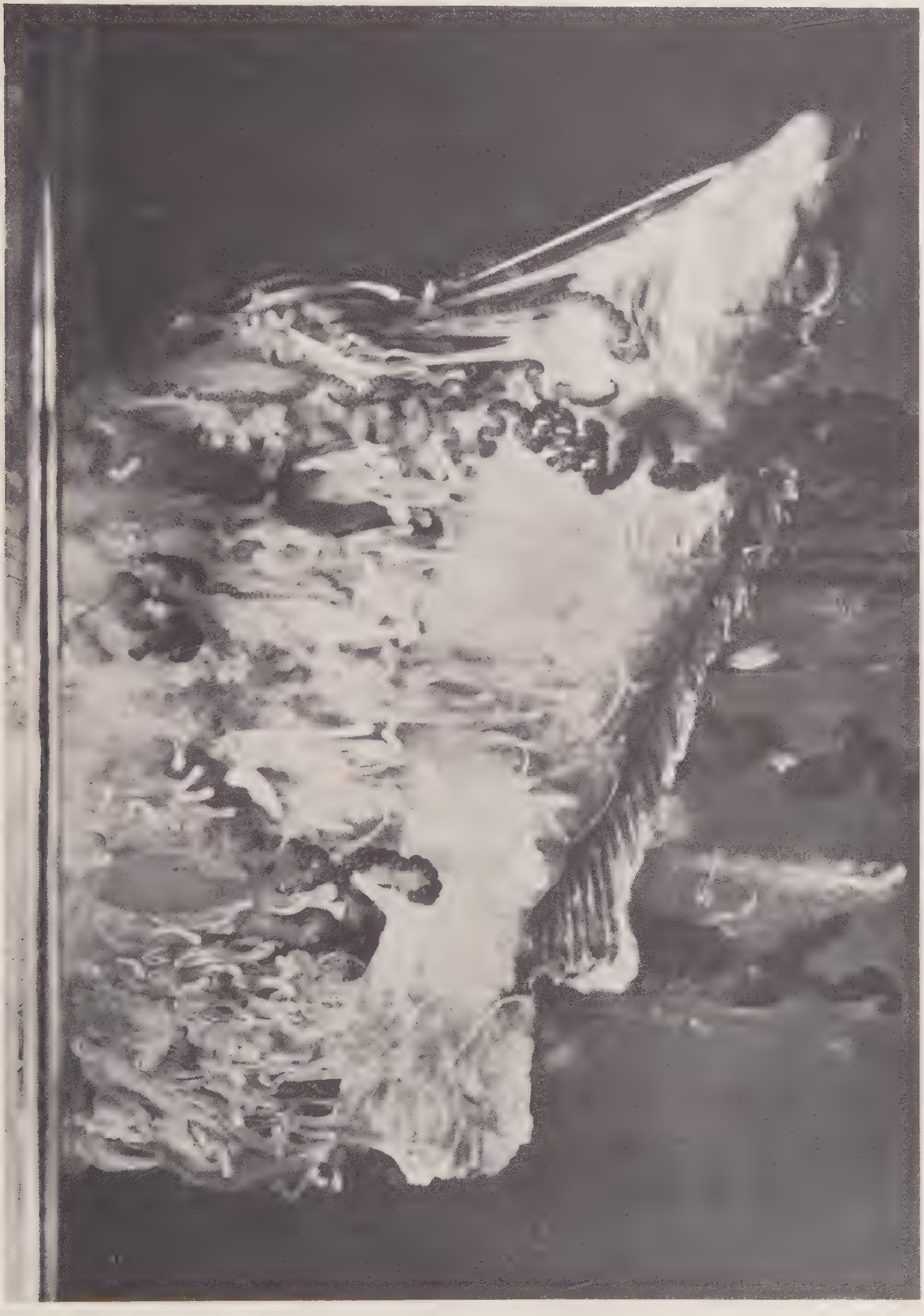


Physalia catching a fish.



Physalia eating a fish.

PLATE III.



Gastrozooids of Physalia attached to a fish.

THE INTERTIDAL ECOLOGY OF SELECTED LOCALITIES IN THE PLYMOUTH NEIGHBOURHOOD

By Ronald G. Evans

Department of Zoology, University College of Wales, Aberystwyth

(Text-figs. 1–14)

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Introduction

The importance of surf action, both as a presence or absence factor and as a modifying influence on the nature of littoral distribution, has been demonstrated during a survey of intertidal conditions in Cardigan Bay (Evans, 1947). The coast of mid-Wales, however, is comparatively smooth in outline, and offers little variation in exposure to or shelter from wave-action; consequently it was decided to confirm and amplify certain features of the previous study by the investigation of a much more irregular coastline in the neighbourhood of Plymouth. Here (see Fig. 1) the nature of the coastline is such that localities exposed to maximum wave action and localities almost completely sheltered from surf both occur within a short distance of each other. The extent to which wash, splash, and spray, resulting from heavy surf, may modify the vertical ranges of intertidal plants and animals is known in a general way only; it is here proposed to treat this problem with more attention than it has hitherto received, and to record, if possible, the actual extent to which such modifications may be observed. It is known that splash and spray, by raising the effective (in distinction to the predicted) level of tides, both tend to raise

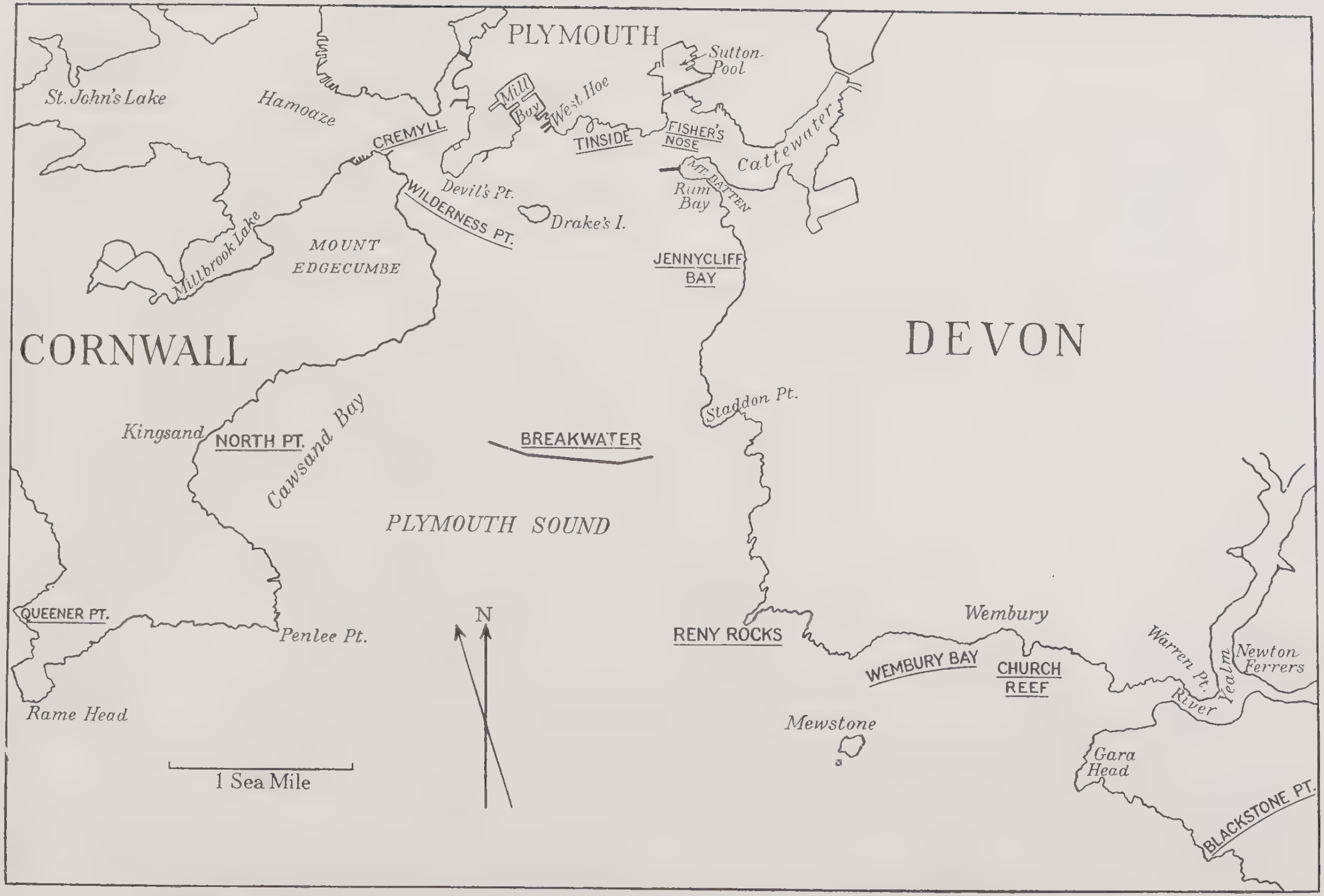
PLYMOUTH
Sutton Pool
St. John's Lake
Hamoaze
Mill Bay
West Hoe
CREMYLL
TINSIDE
FISHER'S NOSE
Cattewater
MT. BATTEN
Rum Bay
Devil's Pt.
Drake's I.
WILDERNESS PT.
JENNYCLIFF BAY
MOUNT EDGECUMBE
Millbrook Lake
CORNWALL
DEVON
Staddon Pt.
Kingsand
NORTH PT.
Cawsand Bay
BREAKWATER
PLYMOUTH SOUND
N
QUEENER PT.
Penlee Pt.
RENY ROCKS
Wembury
WEMBURY BAY
CHURCH REEF
Warren Pt.
Yealm River
Newton Ferrers
Rame Head
Mewstone
Gara Head
BLACKSTONE PT.
1 Sea Mile

Fig. 1. Map showing localities included in the survey. (After *Plymouth Marine Fauna*, 1931.)

the upper limit of certain species with regard to predicted tidal levels. Moore (1935*a*) has shown that surf also has a lowering effect on the lower limit of *Balanus balanoides*, but whether similar effects may be distinguished in other species remains uninvestigated, and it is proposed to consider this possibility.

Furthermore the existence of 'critical levels' will be examined. It was found (Evans, 1947) that such levels in Cardigan Bay appear to be rather different in position from those described by Colman (1933) as being critical for species on Church Reef, Wembury, and before a true comparison could be made it was decided that this latter area must be restudied more extensively than Colman's traverse-method made possible. Moreover, the position of such critical levels under different local conditions (e.g. of surf action and rock-configuration) is likely to prove interesting.

Finally, by making an extensive study of Church Reef, and comparing the results with those obtained by Colman (1933), it will be possible to obtain some idea of the extent to which the study of a few detailed traverses can give an average picture of distribution in such an area.

The work was carried out in the summer of 1946; twelve localities in the Plymouth region were selected, and the distributions of some of the common plant and animal species were examined and described at each locality.

List and Description of Localities Visited

These are all shown in the map (Fig. 1), with the exception of Fort Charles and Bolt Head, which lie in the Salcombe estuary, almost 20 miles to the east of Plymouth Sound.

Bolt Head. This lies on the west of the entrance to Salcombe estuary and is open to winds and waves from any quarter between east and west. Even when the wind is not strong the swell is appreciable, and the wash, splash, and spray zones are quite extensive. The cliff face is high and the rocks slope steeply down to low water, these slopes generally facing south-south-west and receiving both maximum surf and maximum illumination. Near low-water mark the steep faces tend to flatten out horizontally in some places. Very little loose material occurs, except for a few large boulders or slabs which are occasionally found wedged in narrow crevices.

Blackstone Point. Just east of Gara Head (see Fig. 1), this is open to the sea from west to east-south-east, with some little protection on the east from Revelstoke Point and other points on the peninsula. High jagged ridges of Dartmouth Slate slope almost vertically to low water, sometimes from a height of over 50 ft. above chart datum. Deep fissures, running approximately north-south, occur between the slate laminae, which present almost sheer faces to the east and west. Here again considerable surf action is experienced.

Reny Rocks. This group of rocks, on the east side of the entrance to Plymouth Sound, is exposed to winds between west and east-south-east. Moreover, Rame Head lies some distance away on the west, and its sheltering effect is small; the same is true of Gara Head and the Mewstone on the east and south-east. The locality is almost as fully exposed, therefore, as Bolt Head or Blackstone Point. Reny Rocks consists of a group of irregular, steep-sided peaks, rising to over 40 ft. above low water, and separated from the mainland by a low-lying stretch of boulders which dries out at mean low water of neaps. (Owing to the inaccessibility of the Rocks except at low water, this area was not investigated as thoroughly as the other localities.)

Queener Point. Rame Head itself was inaccessible owing to the presence of anti-invasion defences, consequently Queener Point, on its north side, was chosen for investigation. This is less exposed than Rame Head itself or than Bolt Head, Blackstone Point, or Reny Rocks, being open to the sea only from south to west-north-west. However, the rocks are steep and jagged, rising to 30–40 ft. above chart datum, and running approximately north-east to south-west; and since the swell is usually heavy, a considerable amount of wash, splash, and spray is experienced. Large pebbles and boulders occur in the gullies between the rocky promontories, and on the north and north-west sides of the Point the steep rock levels out to a horizontal stretch just below mean tide level.

Plymouth Breakwater. An artificial structure, lying across the entrance to the Sound, at approximately 2 miles from the mainland, this is composed of limestone blocks, with large masses of rough concrete in front. These concrete masses are cubical blocks, 10–12 ft. square, with their bases at low water. They are separated from each other by approximately 6 yards, and from the south slope of the Breakwater by about 15 yards of a fairly level stretch of loose limestone blocks with boulders wedged between them. The whole Breakwater is described in detail by Lysaght (1941). An area in the centre was chosen for investigation, including about 30 yards of the south and north slopes, the top, the sheltering blocks and the level area behind these. The locality is open from south-west to south-east, with some protection outside this quadrant from Penlee and Reny Points. Wave action is strong on the south slope, but the protecting blocks afford some shelter to the lower part of this slope. The north side is, in comparison, fairly sheltered.

Tinside to West Hoe. Here the rocks are of limestone, broken and fissured and generally descending rather steeply to low water. The surface is pitted with the holes of boring organisms (e.g. *Saxicava rugosa*), and depressions and rock pools are frequent. Caves and inlets occur along the front, and the natural line of the rocks is interrupted by artificially built concrete walls, steps, quays, etc. Pebbles and boulders are present in coves and channels. The Breakwater, lying about 2 miles offshore, gives comparatively little shelter and a heavy swell is common in the waters of the Sound when the wind is in the south. This, combined with the steep slope of the Tinside rocks, makes for fairly heavy wave shock, but the area is less exposed than those previously described. Towards the east end, in the Fisher's Nose region, the shelter of Mount Batten breakwater (about a quarter of a mile south) begins to be felt, also the shore is less steep here, and the surf is mitigated to some extent.

Church Reef, Wembury. Colman (1933) studied only the landward portion of this locality, but the present survey also includes the steep seaward reefs and ridges. The area is very irregular, the angle of dip of the rocks is generally steep and the slopes face seaward, but this is variable. High peaks, which are not completely submerged even at high springs, occur on the south and south-east, but on the north, north-west and north-east corner the general lie of the shore is lower and more regular. The centre of the Reef is occupied by high peaks (e.g. Colman's 'Central Rock'). Pools, inlets, and channels are frequent, often containing shingle and gravel, but large boulders are not common. At the top of the shore the cliff face is low and is footed by shingle on the west, but on the east the shingle disappears and a mass of steep rocks occurs (through which runs Colman's 'Traverse D'). As a whole Church Reef may be described as moderately exposed to surf, receiving some shelter on the west from Reny and Wembury Points, on the south-west from the Mewstone, and on the east from Gara Head. Local variation in wave action is experienced; the south faces of the low-tide reefs are battered by heavy surf, but they create some shelter for the more landward portion of the area.

North Point. This lies just east of Kingsand village on the west side of Plymouth Sound, and the area faces almost due south-east. The rocks are felsite, weathering into rounded contours, with few deep fissures, unlike the Mica-schists of Bolt Head, for example. The beach is much more regular than it is at any of the other stations, and the slope is fairly even, while no peaks or high ridges are present, and vertical faces are occasional only. Gravel and shingle are present in pools and gullies. Penlee Point, on the south, provides some shelter, so does Reny Point on the east-south-east, but North Point is open to the sea between these two headlands. It may be described as moderately exposed to surf, and the regularity of the rock formation reduces the range of variation in shelter and surf action.

Jennycliff Bay. This is an area on the east side of Plymouth Sound, between Rum Bay on the north and Ram's Cliff on the south. The strata of Staddon Grits weather into small but steep headlands, with intervening areas of lower rock. In these low-lying areas occur boulders and small loose masses from the cliff face, while sand and gravel are present locally. The general dip of the rocks is seaward, but this varies. Though actually enclosed from the open sea on all sides, Jennycliff Bay is not very sheltered; the west side of the Sound and the Breakwater both lie some distance away, and surf action is strong when the wind is in the south, west or south-west. Local variation is again experienced; the level areas are protected by the headlands, and the south and south-west aspects of higher rocks receive the maximum of wave shock. In general, the area may again be considered as moderately exposed.

Fort Charles, Salcombe. This lies just south of Salcombe village on the west side of Salcombe estuary, and faces almost due south. Two distinct areas were investigated here; Fort Charles east and Fort Charles west. On the east side (i.e. Fort Charles east) the high cliff face descends steeply to a narrow shingle beach which, a few yards further seaward, rises sharply to a high mass of rocks on which stands a ruined fort. In front of this ruin the rock steps irregularly down to about high-water neaps level, then drops perpendicularly to low water. Offshore, a few small reefs of lower rock occur. On the west side (Fort Charles west) the cliff descends to a jumbled mass of loose rock, passing into a zone of low-lying ledges with scattered boulders, which continues about 50 yards to low water. Here there are no peaks or steep-sided rocky masses of any size. The whole of the Fort Charles locality is open to the sea only between south-south-west and south-south-east; moreover, the shallow estuary and large sandbanks also tend to reduce the violence of surf. However, the high steep rocks of Fort Charles east are more subject to wave shock than the comparatively level shore of Fort Charles west.

Wilderness Point. This is an area just east of the Cremyll landing stage, facing slightly east of north. The rock is a continuation of the Plymouth limestone, and similar to it in texture. The shore is backed by a high stone wall, and the upper beach just below this consists of rocky peaks, 4 or 5 ft. high, surrounded by shingle. Proceeding down the beach shingle becomes less abundant and the rocks flatter and more regular. The area is enclosed from the open sea on all sides, and neither surf nor swell is experienced to any appreciable extent. The water is laden with suspended material brought down the Hamoaze, and fucoids tend to trap and filter this, and to lay a deposit of fine silt over the rocks of Wilderness Point.

Warren Point. This area lies on the north bank of the river Yealm, about a mile east of Church Reef, and faces south. The cliff face is very low and drops to a stony beach with patches of mud and silt. In places rock ledges protrude through the shingle to as low as extreme high-water neaps level, but usually the rock is covered by shingle from above this level down to low water. The locality is enclosed from the open sea on all sides, and wave action is at a minimum; although the beach is stony, the pebbles are not liable to much movement, and are sufficiently stable to support several plant and animal species.

In addition to the foregoing localities which were studied in detail, notes were also taken at other points on the shore, e.g. in Wembury Bay, at Cremyll, at Newton Ferrers, etc.

It is unfortunate that there exists no adequate means of measuring the degree of exposure to wave action to which various localities may be subjected. Moore (1935*a*) has attempted to do this on a basis of 'the number of days per hundred days in which any wind blows into the exposed aperture of the locality in question'. While this may give some indication of the maximum exposure which can be expected at a given station on the coast, there exists, within each locality, such a degree of variation that the method becomes impracticable in a survey such as the present one. Within an irregular formation of rock such as Church Reef, for instance, some rock faces (e.g. the south faces of the seaward reefs) will be as exposed to surf almost as heavy as that experienced at Bolt Head, while other stretches in the same locality (e.g. flat rocks to the leeward of high ridges) will be as sheltered from the full force of the waves as the shore of Wilderness Point, for example. So many factors combine to produce this variation that it is impossible to derive any satisfactory expression of relative wave-exposure on a given surface. Taking into account the orientation of the rock with regard to the waves and the direction of the prevailing winds, the angle of slope, its proximity to sheltering masses, and its position with regard to tidal levels (see later), it is, however, possible to form some idea of the exposure to which a small area is likely to be subjected. The twelve localities listed above are arranged in order of increasing shelter, the list given in Table I

TABLE I. LIST OF STATIONS NUMBERED IN FIGS. 3–12 ARRANGED IN ORDER OF DECREASING EXPOSURE TO WAVE ACTION

1.	Bolt Head. Vertical south face	‘Very exposed’
2.	Reny Rocks. Vertical south face	
3.	Blackstone Point. Vertical east and south-east faces	
4.	Queener Point. Vertical south face	
5.	Blackstone Point. 50° slope facing east	
6.	Church Reef. South face of seaward reefs	
7.	Breakwater. South slope	
8.	Bolt Head. Horizontal rocks	‘Exposed’
9.	Queener Point. Horizontal rocks	
10.	Blackstone Point. North-west face	
11.	Bolt Head. North-east overhang	
12.	Church Reef. North face of seaward reefs	
13.	Jennycliff Bay. Vertical south and south-west faces	
14.	Tinside. Vertical south face	
15.	Blow-hole in Wembury Bay	
16.	Church Reef. Landward rocks	‘Semi-exposed’
17.	Church Reef. Protected south face	
18.	Church Reef. Flat rocks on north-east	
19.	North Point. East end	
20.	Jennycliff Bay. 70° slope, facing east	
21.	Breakwater. North face	
22.	Tinside. 40° slope, facing south	
23.	Fort Charles. East	
24.	Jennycliff Bay. North face and overhangs	‘Sheltered’
25.	Bolt Head. Cave	
26.	Jennycliff Bay. Flat rocks	
27.	Fort Charles. West	
28.	Breakwater. Corner on north face	
29.	Tinside. Horizontal rocks	
30.	Tinside. Fisher’s Nose region	
31.	North Point. West end	
32.	Wembury Bay. Sheltered south face	
33.	Wembury Bay. North face	
34.	Cremyll	‘Very sheltered’
35.	Wilderness Point	
36.	Warren Point	
37.	Newton Ferrers	

includes all the areas quoted in the paper and indicated by number (e.g. [26]) in Figs. 3–12; these also are arranged in order of decreasing exposure (based on the considerations cited above), and, for convenience, have been classified into five categories, 'very exposed', 'exposed', 'semi-exposed', 'sheltered', and 'very sheltered'.

CLIMATIC FACTORS, TIDAL LEVELS, AND METHOD OF INVESTIGATION

The climate of Plymouth is mild, and typical of south-west England in general. According to Lysaght (1941), on an average 33% of the winds blow from between south-west and south-east, i.e. from the Channel and from the open Atlantic. Thus, as in Cardigan Bay, the main exposure is from a southerly direction, but from personal observation it is confirmed that such headlands as Bolt Head, Blackstone Point, Reny Point, and Queener Point, are very much more surf-beaten than any locality in the middle of Cardigan Bay. On the other hand, both Wilderness and Warren Points receive far more shelter from waves than any locality on the coast of mid-Wales.

Tidal data are taken from those given for Devonport in the Admiralty Tide Tables, Sect. A, Pt. I, and values for extreme springs and neaps are means for the 10 years 1937–46. The Devonport figures are taken as applicable for all localities except Bolt Head and Fort Charles; for these, the corrections for Salcombe tides are applied. Table II gives the tidal scales for both Plymouth and Salcombe localities, but in the following text-figures the zonations at Bolt Head and Fort Charles are interpolated (with the necessary corrections) on the Plymouth scale, for purposes of comparison. All heights are given as feet above or below Chart Datum which, at Devonport, lies 8·42 ft. below Ordnance Datum.

TABLE II. TIDAL SCALES

(Heights are given as feet above or below Chart datum)

Tidal level	Plymouth (ft.)	Salcombe (ft.)
E.H.W.S.	17	17·3
M.H.W.S.	15·7	16
M.H.W.N.	12·3	12·6
E.H.W.N.	10	10·3
M.T.L.	8·2	8·8
E.L.W.N.	5·7	6·6
M.L.W.N.	4·6	5·5
M.L.W.S.	0·2	1·1
E.L.W.S.	−1·6	−0·7

The species selected for attention are those studied in the Cardigan Bay survey (Evans, 1947), but *Himanthalia lorea* (de la Pyl) and *Balanus perforatus* Brugière are additional. *Sabellaria alveolata* (L.), which is not general in the Plymouth neighbourhood, is omitted.

Methods similar to those adopted in the previous survey were followed, i.e. tidal levels were marked by observation of the water-level at different times between high and low water, and zonation was studied by walking along the shore and taking notes, parallel to the water-line, first at one level and then at another as the tide ebbed. In view of the limited period available for the work one innovation was introduced; advantage was taken of an early period of calm weather to mark reference levels at as many stations as possible, the time of marking of the water-level being noted and its height being calculated by using Supplementary Table I of the A.T.T., Sect. A, Pt. I. This procedure has the following advantages. (*a*) Providing that all the localities are marked during one day or during days of similar conditions of wind and tides, then any error in the height of the marked levels will tend to be a constant one, for comparative purposes. The Breakwater, Queener Point, North Point, Wilderness Point, and Jennycliff Bay were all marked during one calm day, and Tinside in the late evening of the same day. Reny Rocks, Church Reef and Warren Point were visited on the following day. A break in the weather delayed the marking of Blackstone Point until a fortnight later, while Fort Charles and Bolt Head were marked on successive days at the same period. (*b*) Having once established such reference points during calm weather, the areas could be studied even when the condition of the sea was not ideal; the actual height of the tide, at the calculated time when it should arrive at the mark, could be checked with reference to this mark, and an approximate estimate of any error due to wind or swell could be made.

The efficiency of this method of assessing vertical heights on the shore and the zonation of species may be judged by comparing results obtained for the zonation of the algae on Church Reef with similar figures obtained from a study of the same area from detailed levelled traverses by Colman (1933). This comparison is made in Fig. 2; it should be noted that the writer has deducted Colman's 'splash allowance' of 2 ft., and has also based the zonation on the tidal scale given in Table I (i.e. using 10-year means for extreme neaps and springs). There is a surprising measure of agreement, though certain points demand comment. While my limits for the 'zones of abundance' of *Pelvetia*, *Fucus spiralis*, and *Ascophyllum nodosum* agree closely with Colman's 'mean limits' of distribution (1933, p. 454, table IV), my absolute limits of distribution are more extended than the latter's 'extreme limits'. Especially is this so for *Pelvetia* and *Fucus spiralis*, both of which, it should be noticed, are zoned by Colman on one traverse only (Traverse D); for *Ascophyllum* and *Fucus serratus*, which he zones on two traverses, the differences are less marked. This appears to be the natural result of a more extensive and broader survey; but, allowing for this, the direct observational study of tide levels and the basing of vertical zonations on this would seem to be at least as accurate as any method based on the detailed examination of surveyed traverses. This is further indicated by the general consistency of the results which the writer has obtained in different areas, both on the coast of mid-Wales and in the Plymouth locality. Thus, if the necessary precautions with regard to calm conditions are observed, the method appears to be fully justifiable, and possesses undoubted advantages for this type of survey.

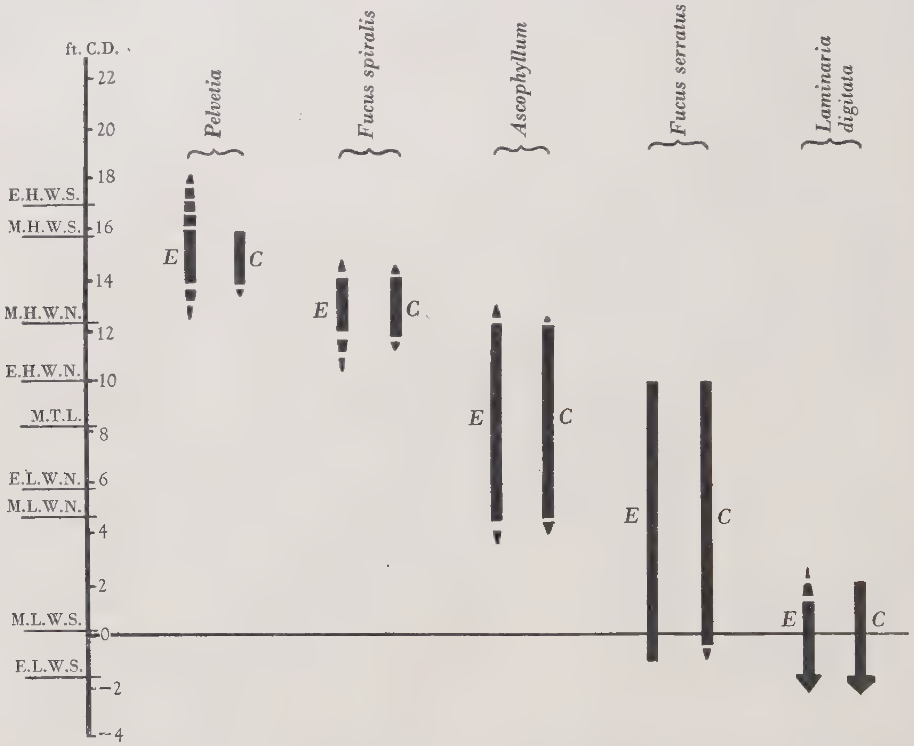

Fig. 2. Comparison of algal zonation on Church Reef, Wembury, with results obtained by Colman (1933). *E*, present results; *C*, Colman's data.

Note. In Figs. 2–14 inclusive the same scale is used for vertical heights above or below chart datum.

RESULTS

The general features of the horizontal distribution of the species studied (with the exception of *Himanthalia lorea* and *Balanus perforatus*) as they occur in Cardigan Bay have been fully discussed in my earlier paper, together with the effects of wave action and other factors on this distribution. The present investigation confirms many of these observations, which it is unnecessary to repeat here, except where any significant differences have been noted.

Flora

Pelvetia canaliculata Dcne. & Thur. This is entirely absent from Bolt Head, and represented only as occasional and very stunted plants at Blackstone, Reny, Queener, the Breakwater, and Tinside. A sparse and scattered *Pelvetia* zone

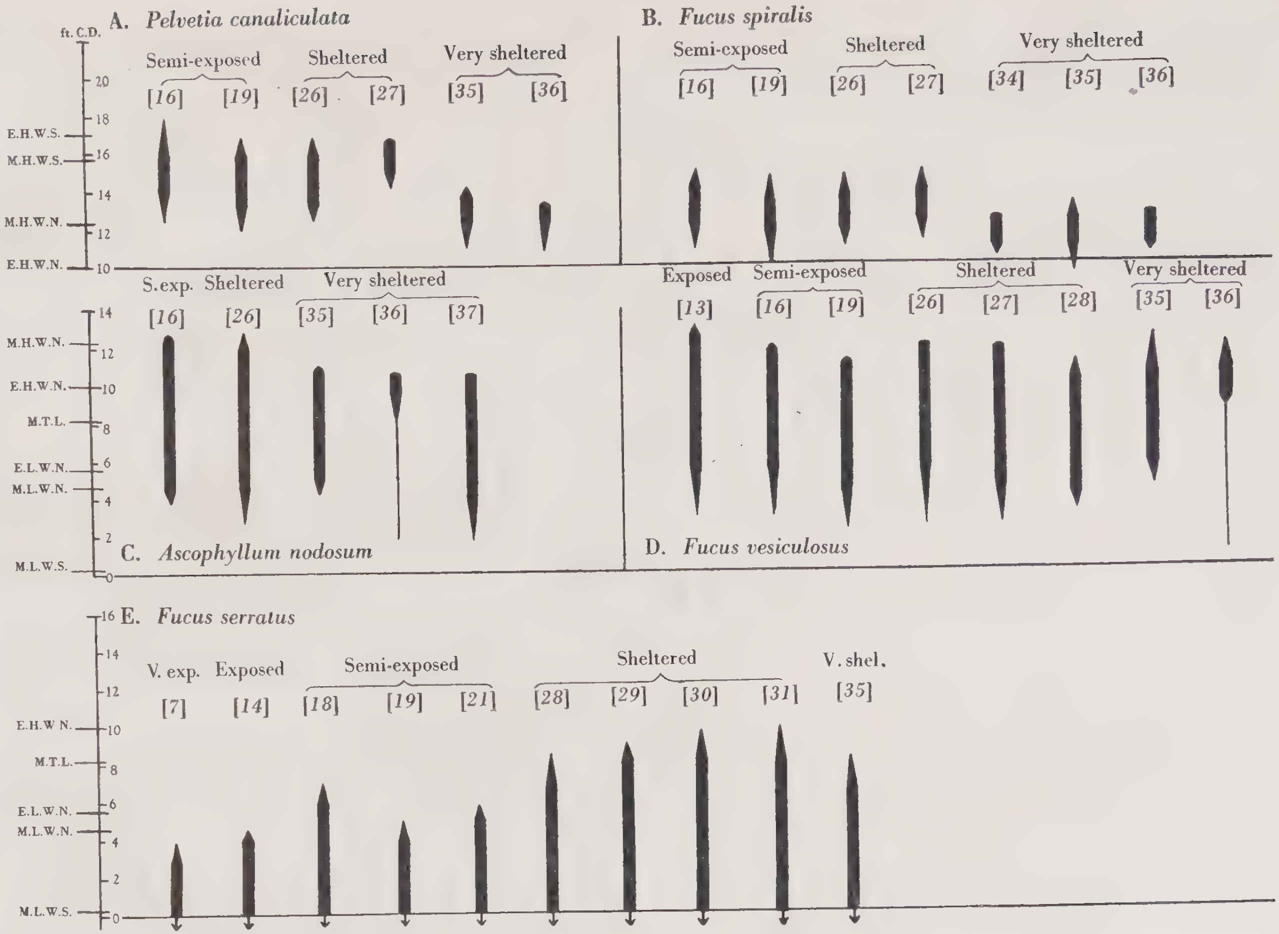

Fig. 3. Zonation of *Pelvetia* (A), *Fucus spiralis* (B), *Ascophyllum* (C), *Fucus vesiculosus* (D) and upper limit of *F. serratus* (E) at different localities.

may be recognized on the landward rocks of Church Reef; this improves on the more regular rocks of North Point, and is fairly good at Jennycliff, Fort Charles west and Wilderness Point. Under the very sheltered conditions of Warren Point the zone is excellent, the growth is thick, the plants are robust, they are not confined to the deeper cracks in the rock surface, and are easily detached by hand. Fig. 3A summarizes the vertical distribution of the alga, and the lowering of the *Pelvetia* zone with increase in shelter (i.e. from Church Reef [*16*] to Warren Point [*36*]) is marked. At most of the localities the presence of shingle and other loose material is obviously unfavourable to *Pelvetia*, but at Warren Point wave action is so reduced that the pebbles are not moved to any appreciable extent, and the adverse effect of shingle is not felt to the same extent.

Fucus spiralis L. is entirely absent not only from Bolt Head, but also from Tinside, and is less frequent than *Pelvetia* at Reny, Queener, and Blackstone Points. Like the latter alga, however, *Fucus spiralis* first occurs as a recognizable zone on Church Reef, and improves with increasing shelter to Warren Point, Cremyll, etc. Again the effect of wave action on the height of the zone may be recognized. Comparing Figs. 3A and 3B there is an obvious correlation between the upper limit of *F. spiralis* in quantity and the lower limit of the *Pelvetia* zone. Where both algae grow thickly, very little mixing occurs, but where the algae are thin and sparse then a certain amount of mixing may occur. Similar conditions are found in Cardigan Bay.

Ascophyllum nodosum Le Jol is absent from Bolt Head, Blackstone, Reny, and Queener Points, from the Breakwater and Fort Charles east, and is very occasional only at North Point, Fort Charles west, and Tinside. Under shelter in the Hamoaze (e.g. at Cremyll and Wilderness Point) and in the Yealm (e.g. at Warren Point and Newton Ferrers) *Ascophyllum* is excellently developed, forming a mid-beach community of robust and long-fronded plants. In Jennycliff Bay and on Church Reef the species is locally well represented, but is poor or absent on exposed rocks, and it is clear that considerable shelter is required before a thick carpet of *Ascophyllum* can be developed. The restriction of the alga to rocks and larger boulders is very marked, and except at Warren Point the species is normally replaced by *Fucus vesiculosus* on smaller stones. On Church Reef *Ascophyllum* is best developed on level areas and is generally poor on steep faces, yet at Newton Ferrers it grows thickly on steep slopes, and in the Hamoaze (e.g. at Admiral's Hard) the weed can exist on vertical quay walls. Tolerance of steep slopes increases as shelter increases, but even on horizontal rock a certain amount of shelter is required by the alga (e.g. the flat rocks of North Point are not carpeted by a thick growth of *Ascophyllum* as surf is still too strong here). The vertical zonation of the alga lies between M.H.W.N. and M.L.W.N., generally speaking (Fig. 3C), but the upper limit is again higher under conditions of moderate wave action (e.g. Church Reef, Jennycliff Bay) than under conditions of extreme shelter (e.g. Newton Ferrers). There is a correlation between the upper limit of *Ascophyllum* and the lower limit of *Fucus spiralis*, especially where both zones are thick (e.g. Warren Point, Cremyll, etc.), but where the shore rock is irregular this demarcation is not nearly so obvious. The lower limit of *Ascophyllum* varies, but the alga appears to be capable of existing at least as low as M.L.W.S. + 2 ft., though it is generally abundant only above M.L.W.N. Gislén (1930) describes the species as extending lower in sheltered and unclean waters, possibly this explains its low lower limit in the Yealm estuary.

Fucus vesiculosus L. Though not entirely absent from any of the stations visited, this alga is extremely poorly represented at Bolt Head, Blackstone, Reny, and Queener Points, and on the south face of the Breakwater. At all these localities *F. vesiculosus* is found only as occasional and tattered plants in cracks on the exposed slopes. On Church Reef the alga is generally less well developed than *Ascophyllum*, but it often tends to replace the latter on the steeper slopes. At Fort Charles west and in parts of Jennycliff Bay *Fucus vesiculosus* may form a fairly pure (i.e. unmixed with *Ascophyllum*) community on the less regular stretches of rock and boulders, but at Wilderness and Warren Points it is definitely dominated by *Ascophyllum*. As in Cardigan Bay, *Fucus vesiculosus* is more tolerant of broken ground, of boulders, of steep faces, and of surf than *Ascophyllum*, and peaks and boulders lying in a thick carpet of the latter alga may be dominated by *Fucus*. The writer has suggested previously (Evans, 1947) that the general infrequency of a thick, pure community of *F. vesiculosus* may be due to the rather sharply set optimum of surf conditions necessary for this; where surf action is too strong the alga occurs merely as isolated plants and clumps, where shelter is pronounced then *Ascophyllum* is developed and competes successfully against *Fucus* for dominance. Generally *F. vesiculosus* is not found much above M.H.W.N. (Fig. 3D), but may occur above this under the influence of splash. It tends to occur to higher levels than *Ascophyllum*, however, which is the reverse of what has been described in Cardigan Bay. The lower limit of abundance lies generally in the region of E.L.W.N. to M.L.W.N., but where the *Fucus serratus* zone is well represented *F. vesiculosus* may be dominated by this alga from E.L.W.N. down. The presence of a stony lower beach at Warren Point prevents both this species and *Ascophyllum* from being anything more than occasional from E.H.W.N. down at this locality, but isolated plants of *Fucus vesiculosus* have been taken here as low as M.L.W.S. + 0·5 ft.

Fucus serratus L. As described by most workers, this species requires horizontal or gently sloping rock and a fair amount of shelter from surf, but when shelter is pronounced it may occur on steep slopes, and it may be absent even from a level beach where surf is too violent. The *F. serratus* zone is well represented on Church Reef (except on the seaward slopes of the outer reefs), at Tinside, North Point, Jennycliff, and Fort Charles west; and it achieves its maximum development at Wilderness Point, but the stony lower beach at

Warren Point is again unfavourable. The lower limit of distribution at all localities lies below M.L.W.S., but the lowest level to which the writer has taken the species lies in the region of M.L.W.S. – 1 ft. (at Church Reef, Jennycliff, North Point, and the Breakwater). The absolute upper limit of distribution under optimum conditions (e.g. in the Fisher's Nose region of Tinside [*30*] and at the west end of North Point [*31*]) is E.H.W.N., but the upper limit of abundance is variable. From Fig. 3E it will be seen that the upper limit of the *F. serratus* zone is very markedly affected by the intensity of surf. At Bolt Head and Blackstone Point no distinct zone can be recognized; on the south Breakwater slope [7] the zone extends up to M.L.W.S. + 3 ft. only, but with increasing shelter at different localities this upper limit moves up the shore until, at North Point west end [*31*] (for example) it is as high as M.T.L. Further reduction in wave action, and in the height of wash and splash, results in a subsequent lowering of this upper limit (e.g. at Wilderness Point [*35*]). The ten localities figured in Fig. 3E are chosen from a large selection of data all showing the same general principle, i.e. that with decreasing surf *F. serratus* is enabled to exist higher and higher up the shore, but after a certain optimum is reached, further reduction in wave action results in a slight lowering of the upper limit.

Himanthalia lorea Lyngb. This occurs in much more wave-beaten localities than any of the other fucoids, and as Rees (1935), Gibb (1938), and others state, it is characteristic of moderately wave-beaten situations. *Himanthalia* is well represented at Bolt Head, Blackstone, Reny, Plymouth Breakwater, and Church Reef; at North Point it is less frequent; at Fort Charles and Wilderness Point it is occasional only. Fischer-Piette (1936) comments on the paucity of the species in bays such as Lyme Bay, and notes its abundance on projecting headlands with deep off-shore water. He suggests that this may be due to the generally heavy sedimentation of bay water, resulting in a poor penetration of light. This would explain not only the scanty development of *Himanthalia* at Fort Charles and Wilderness Point, but also its absence from Cardigan Bay, for the species can exist much further north than this (Kitching, 1935). *Himanthalia* appears to favour fairly gentle slopes (e.g. on the level stretch behind the protective blocks of the Breakwater there occurs an excellent zone of this alga). On Church Reef, characteristic fringes of *Himanthalia* are found at the bases of exposed 45° slopes which are thickly covered with barnacles and bare of all other fucoids. Kitching (1935) agrees that the species can inhabit slopes up to 80° but that it usually prefers more level ones, and it was only occasionally found on vertical landward faces and on steep gulley banks. Gibb (1938) describes a *Himanthalia* zone between that of *Fucus serratus* and the Laminarians, but in the Plymouth neighbourhood such a zone is best observed where *F. serratus* is poor or absent. Thus, on the south face of the Breakwater [7], *Himanthalia* is definitely the dominant alga up to 1 ft. above the Laminarian zone. On the other hand, where the *Fucus serratus* community is well developed (e.g. at Jennycliff and North Point), *Himanthalia* mixes with this alga, and no separate belt can be distinguished. The species is common to below E.L.W.S. and its upper limit lies in the region of M.L.W.N. (see Fig. 4A), though occasional plants were taken on a north-facing, shaded slope as high as E.L.W.N. at Bolt Head [*1*]. The upper limit of abundance is highest on Church Reef [*6*] and in Jennycliff Bay [*13*], while under the extreme exposure of Bolt Head [*1*] the alga is not common above M.L.W.S. + 1 ft. (though it is occasional to E.L.W.N.), and the height of the *Himanthalia* zone, like that of *Fucus serratus*, appears to be limited by the degree of surf action.

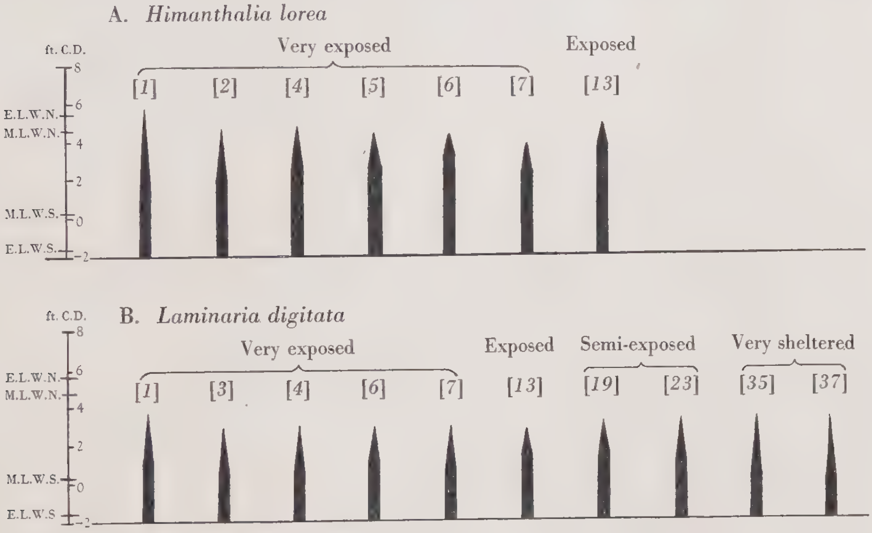

Fig. 4. Upper limits of *Himanthalia lorea* (A) and *Laminaria digitata* (B).

While adult plants are not usual above M.L.W.N., vegetative 'buttons' may be found much higher, e.g. up to M.T.L. or above on the Breakwater blocks, or even to E.H.W.N. under a thick carpet of fucoids.

Laminaria digitata Lamour. This occurs in quantity at all the stations visited, except on the stony beach of Warren Point, and is tolerant of a wide range of conditions of surf. The absolute upper limit of distribution lies just below M.L.W.N. (see Fig. 4B), but the alga is not common (i.e. the 'Laminarian zone' does not commence) much above M.L.W.S. This zone may begin as high as M.L.W.S. + 2 ft., e.g. on the flatter rocks on the west side of Queener Point where, although surf action and wave crash are not excessive, there is generally a heavy swell and a broad wash zone. Under conditions of extreme exposure it may not extend much above M.L.W.S. + 1 ft.; on the other hand, where shelter is very pronounced *L. digitata* may not be common above M.L.W.S. Thus the relation between the upper limit of distribution and the intensity of surf, which was demonstrated for *Fucus serratus* and *Himanthalia*, holds good for *Laminaria digitata* also. The effect of slight shelter in allowing the alga to ascend above M.L.W.S. has been noted by Rees (1935), who states with regard to *L. digitata* (p. 93): 'With increasing shelter this alga is no longer confined to channels but spreads out as a belt on the top of the sublittoral, beginning on flat ledges but later, with increasing shelter, occurring as a zone above *Laminaria Cloustoni* on surfaces that do not slope too steeply.'

Laminaria saccharina Lamour. As is general in Cardigan Bay and elsewhere, this species is intolerant of excessive exposure to wave action, and it is confined to pools and channels at Bolt Head, Church Reef, Reny, etc. It was never found as commonly as *L. digitata* at any of the stations visited. At Warren Point a few washed-up specimens were taken, measuring up to 2 yards long, but attached to stones only a few inches in diameter, which is a further evidence of the effect of extreme shelter on the stability of such a substratum.

Corallina-lithothamnia association. On steep faces at exposed points such a community may exist in the lower Balanoid zone, in the absence of all other weed associations. Under slightly more sheltered conditions this may be invaded by *Gigartina stellata*.

Gigartina stellata Batt. This alga is well represented in the lower Balanoid zone on the west side of Queener Point, and on the exposed reefs of Church Reef. It is a common constituent, too, of the undergrowth of the *Fucus serratus* zone, while on parts of Church Reef where a typical belt of the latter fucoid is developed, it is common to find steeper faces and protruding ledges in this zone shunned by *Fucus* and colonized by *Gigartina*. It is also more frequent than fucoids on the stony beach at Warren Point. Its upper limit under *Ascophyllum* or *Fucus serratus* may lie as high as E.L.W.N., but little occurs in the open at this level. The lower limit lies beyond E.L.W.S.

Laurencia pinnatifida Lamour. Like *Gigartina* and *Corallina*, this is often common in the undergrowth of a zone of *Fucus serratus*, but also occurs on rocks too exposed for fucoid growth. It is common in patches on rocks thickly encrusted with barnacles, and such *Laurencia-Balanus* communities normally occur above a lower zone of *Gigartina* and barnacles. The upper limit of *Laurencia* at Queener Point lies above M.T.L., but at Bolt Head the alga is restricted to lower levels. It is generally patchily distributed, and does not seem to form a 'continual carpet' such as Rees (1935) describes at Lough Ine.

Porphyra umbilicalis (L.) J.G. Ag. is extremely haphazard in its distribution, occurring from conditions of extreme exposure to those of extreme shelter, and is apparently unaffected by either. Steep, barnacle-encrusted reefs, and smooth boulders are equally well colonized by *Porphyra*, and it is also commonly epiphytic on fucoid algae. Cotton (1912) remarks with regard to the *Porphyra* association: 'Doubtless surf and spray are largely responsible...this does not account for all the differences that have been noted.' Though the alga occurs sporadically from the Laminarian zone to above E.H.W.S. on exposed peaks, it often tends to form well-defined bands of growth on such peaks and slopes. Thus on steep faces at Bolt Head a band was noted in the M.H.W.S.-E.H.W.S. region; on the south face of the Breakwater two such bands were observed, one between M.H.W.N. and M.H.W.S., the other at about M.L.W.N., with practically no *Porphyra* in between. The reason for this is not clear.

Lichina pygmaea Ag. The distribution of this lichen in the Plymouth area has been described by Naylor (1930), and the present survey confirms the major part of her observations. *L. pygmaea* is best developed on steep exposed slopes, with rough or barnacle-encrusted surfaces (e.g. at Bolt Head, Blackstone, Reny, etc.). Yet, provided water movement is strong enough, the lichen is not restricted to vertical faces, but occurs quite thickly on gentle slopes (e.g. at North Point). It was not taken under the sheltered conditions of Warren and Wilderness Points, nor, as Naylor (1930) describes, is it present in Jennycliff Bay. The lichen is normally thickest and most extensive on slopes facing in a southerly direction, but it is commonly well developed even on rough landward faces where these are covered with barnacles; it also occurs in caves and overhangs when these are exposed to strong water movement, and the restriction of *L. pygmaea* to brightly illuminated surfaces as Naylor (1930) remarks is not at all marked. Similar results have been obtained in Cardigan Bay, and the writer is inclined to believe, despite the absence of the lichen from the shaded shore of Jennycliff Bay, that *L. pygmaea* is primarily dependent on surf action and rough rock, and that no simple light effect can be distinguished.

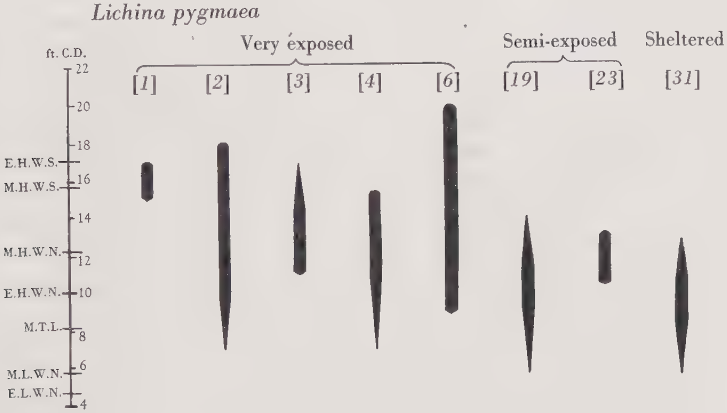

Fig. 5. Zonation of *Lichina pygmaea*.

Naylor (1930) states that the lichen never extends above the *Pelvetia* zone, and generally achieves its lower limit around M.T.L. Only occasionally in the present survey was it taken as low as M.L.W.N., and its lower limit (see Fig. 5) is variable, with no clear relation to surf or any other factor. Where *Lichina* and

Pelvetia are both present (e.g. on the landward rocks of Church Reef, at North Point, and at Fort Charles) the lichen always occurs below the alga (compare Figs. 3A, 5), but with increasing exposure to waves the *Pelvetia* zone disappears and the upper limit of *Lichina* rises until (e.g. on the seaward peaks of Church Reef) it extends to above E.H.W.S. At semi-exposed localities the upper limit lies in the M.H.W.N.-M.H.W.S. region. The high upper limit of the lichen on the seaward reefs of Church Reef [*6*] is worth noting: though not quite so exposed to surf as Bolt Head, for example, the low position of these reefs on the shore results in them receiving splash and spray even at low water on rough days.

Discussion on the Distribution of Algae

The correlation between the intensity of wave action and the distribution of littoral algae is as well marked in the Plymouth area as it is in Cardigan Bay and on British coasts generally. In the course of the present survey it was possible to trace the gradual improvement of weed cover, from the typical 'barnacle areas' of Bolt Head, Blackstone, etc. to the 'fucoid areas' characteristic of sheltered localities (e.g. Wilderness Point). It is a significant fact that this transition, with decreasing intensity of surf, appears to follow a definite pattern, i.e. the process involves a definite invasion of the mid-beach Balanoid zone by fucoids. This invasion proceeds both from low water and from high water towards the centre of the beach, until finally the barnacle belt is more or less obliterated, and a complete scheme of weed zonation (*Pelvetia*, *Fucus vesiculosus*, *Ascophyllum*, *Fucus serratus*, and *Laminaria*) is achieved. Thus (except where it is due to some peculiarity in rock configuration resulting in shelter for the middle of the beach only) one never finds a well-developed fucoid carpet in mid-beach with a barnacle zone above and below it. On the other hand, a mid-beach Balanoid zone passing into fucoids above and below is quite general in semi-exposed situations. Thus at Bolt Head and Blackstone Point, the entire beach from M.L.W.S. upward is occupied by *Balanus* and *Chthamalus*, merging into a zone of *Littorina rudis* and *L. neritoides* at high-water mark, and in such areas there are no intertidal fucoid communities whatsoever. Under slightly more sheltered conditions (e.g. on the west side of Queener Point), not only does the *Laminaria digitata* belt creep up from M.L.W.S. but also *Corallina*, *Gigartina* and *Laurencia* tend to invade the lower part of the Balanoid zone. The next stage is the appearance of a belt of *Himanthalia* above the Laminarian zone, when surf action decreases to the extent it does on the Breakwater and on the seaward parts of Church Reef. Still more sheltered conditions lead to the appearance of *Fucus serratus* as a zone at low water, and the upward extension of this zone, as the intensity of surf decreases, has already been demonstrated (Fig. 3E). Under slightly less sheltered conditions than those required by *F. serratus*, first *Pelvetia* and then *Fucus spiralis* make their appearance at the top of the shore, and the downward extension of the zones of these algae has also been noted (Figs. 3A, B). This is the typical state found in semi-exposed localities, and may be summarized thus: *Littorina* zone, *Pelvetia*, *Fucus spiralis*, barnacles (with scattered plants of *F. vesiculosus*), *F. serratus*, Laminarians. *F. vesiculosus* has been present from an early stage in the transition, but as occasional and tattered plants only; now, as shelter improves, the alga becomes more frequent and the individuals more robust. Still further reduction in the intensity of surf allows *Ascophyllum* to appear; this soon becomes dominant, and where surf is reduced to a minimum (e.g. at Wilderness Point, Newton Ferrers, etc.) the *Ascophyllum* community occupies the mid-beach to the complete exclusion of the Balanoid zone.

Such a process cannot, however, be ascribed to the decreasing energy of surf action alone; were this so, one would expect to find the *Fucus vesiculosus* zone the first to appear, since individual plants of this alga are apparently extremely tolerant of surf. The writer would suggest that not only is the actual force of wave shock important with respect to the algae, but that the relative frequencies with which different shore levels are subjected to wave shock must also be taken into consideration. Stephenson (1941) mentions a suggestion made by D. P. Wilson that the frequency and duration of wave action may determine the upper limits of distribution of low-tide algae, and this certainly appears to be true for *Fucus serratus*, *Laminaria digitata*, etc. (see Figs. 3E, 4B). At the level of M.L.W.S. the shore is comparatively seldom exposed to breaking waves, for during most tides such levels remain submerged; similarly M.H.W.S. and levels above this are only relatively occasionally reached by surf. At M.T.L., however, direct wave shock is experienced twice during every complete tide, and the same is true at all levels between E.L.W.N. and E.H.W.N. From both these levels, proceeding towards low water and high water respectively, there is a progessive decrease in this frequency factor. Both (*a*) the actual force of wave shock, and (*b*) the frequency of this effect will act adversely on the fucoids, and it is reasonable to suggest that the reduction in one of these will mitigate, to some extent, the combined adverse effect of both. Thus, reduction in the factor of intensity of wave force enables *Fucus serratus* (for example) to withstand the frequency factor to a greater degree, and so to exist higher up the shore. (The frequency remains comparatively unaltered, though the intensity of surf will also tend to determine the width of the zone affected by the breaking waves to some extent.) For *Pelvetia* and *Fucus spiralis* at the top of the shore the same argument applies, though since such algae are more limited in their potential depth of zonation than *F. serratus*, the downward extension of these algae with increasing shelter is not so marked as the upward extension of *F. serratus*. Still further reduction in the intensity factor results in still greater tolerance of the frequency factor, and in still further extension of such algae towards mid-beach. Finally the actual force of wave shock becomes so much reduced (e.g. at Wilderness Point) that the frequency with which different shore levels are subjected to breaking waves has little effect, and the entire beach is favourable to fucoid growth.

The presence of weed-free zones in mid-beach has been noted by various workers, and attributed to different causes. Grubb (1936) describes a 'bare zone' between the *F. spiralis* and the *Laurencia-Corallina* associations at Peveril Point, Dorset, and suggests two possible causes. She points out that in this region of the beach (M.H.W.N. to M.L.W.N.) there occurs the maximum fluctuation in periods of submergence and emergence, and that any alga colonizing such levels would need a very adaptable physiology. Secondly, Grubb (1936) remarks that the 'bare zone' is covered or uncovered during the third and fourth hours of tidal flow or ebb, when the rate of water movement is greatest, and that (p. 409), 'this comparatively rapid movement may have something to do with the absence of vegetation here'. Yet the same worker also states (p. 409) that: 'In the sheltered places at Peveril Point...*Fucus serratus* may grow in this region, but for the most part the rocks are too exposed for this species, or for *Ascophyllum*, and since no other species has taken their place, they remain bare.' The presence of *Fucus serratus* in the 'bare zone' at Peveril Point when shelter is experienced is significant, and it appears that this is only another example of what has already been described. Indications of the same phenomenon were noted in Cardigan Bay, but in this locality the range in conditions of exposure and shelter is not wide enough to enable one to describe the process of algal invasion of the mid-beach with the clarity with which it can be seen on the more irregular coastline studied in the present survey. To summarize then, both the actual intensity of wave shock and the frequency of this factor must be taken into account when considering surf effects.

Various opinions have been expressed with regard to the relative tolerance to surf exhibited by the fucoids, especially by *Ascophyllum* and *Fucus vesiculosus*. Both Børgesen (1908) and Zaneveld (1937) appear to hold that the former alga can withstand greater intensity of water movement, but most workers (e.g. Cotton, 1912; Kitching, 1935, and others) take the opposite view. Both David (1941) and the present writer have found *F. vesiculosus* to be the least affected by surf in Cardigan Bay. Cotton (1912) arranges the algae in the following order of decreasing tolerance: *F. spiralis*, *F. vesiculosus*, *Pelvetia*, *Ascophyllum*. Gislén (1930) gives the series as: *Fucus vesiculosus*, *F. serratus*, *F. spiralis*, *Ascophyllum*; while Kitching (1935) gives: *Fucus vesiculosus*, *Pelvetia*, *Fucus spiralis*, *Ascophyllum*. From observations in the Plymouth locality the writer would arrange the algae studied in the following order: 'lithothamnia', *Porphyra umbilicalis*, *Corallina*, *Fucus vesiculosus*, *Himanthalia*, *Laminaria digitata*, *Laurencia pinnatifida*, *Gigartina stellata*, *Pelvetia*, *Fucus spiralis*, *F. serratus*, *Ascophyllum*. This series demands some comment, in view of what has just been said with regard to wave shock and wave frequency. (1) *Fucus vesiculosus* not only exists under conditions of extreme surf intensity, but also at levels where the frequency of waves is at a maximum, and this species must be considered as exceptionally tolerant of the adverse effects of surf. It exists, even, on slopes too exposed for the appearance of *Himanthalia*, *Laminaria*, *Laurencia* or *Gigartina* above M.L.W.S. (2) The apparent intolerance of *Ascophyllum* may be largely due to its position in mid-beach. This would explain a phenomenon previously commented on in the Cardigan Bay investigation, i.e. the presence of solitary and very battered plants of this alga on low-level reefs. Yet it is obviously less tolerant than any of the other fucoids to the factor of wave shock alone, even allowing for the frequency factor. (3) *Pelvetia* exists in a few localities where *Fucus spiralis* is absent, and though its zone is slightly further from the zone of maximum wave frequency (i.e. E.H.W.N. to E.L.W.N.) than that of the latter alga the difference in frequency cannot be very great, therefore *Pelvetia* appears to be the more tolerant of the two species. (4) Both *Fucus spiralis* and *Pelvetia* are more frequent in local shelter at exposed points than is *Fucus serratus*, which therefore appears to be the least tolerant of these three. Here, however, a further complication is introduced. While *Pelvetia* and *Fucus spiralis* spend most of their time above water level, *F. serratus* (and low-level algae in general) is, for the greater part of the time, submerged, and though actual wave crash may not be experienced during the whole of the time of submergence, the effects of back-wash, currents, tidal drag, and swell are likely to be important. (5) *Laminaria digitata* occupies levels which are not often exposed to breaking waves, and it may be argued that its apparent high degree of tolerance of wave shock is due to its low zonation, and that actually it is no less susceptible to this factor than is *Fucus serratus*. But the sharp demarcation between a profuse Laminarian zone and a zone bare of *F. serratus*, which may be observed at many exposed points, does not favour this suggestion, for the factor of wave frequency is not likely to change so sharply within such a narrow vertical range to account for this. Furthermore, the strong holdfast, the leathery and much-divided fronds, and the supple stipe of *Laminaria digitata* would seem to indicate that this species has a very high degree of tolerance of surf. (6) The same is true of *Himanthalia* but, judging from its rather more frequent appearance than *Laminaria* above M.L.W.S., it would appear to be slightly more tolerant than the latter. (7) The ability with which species like lithothamnia, *Corallina*, *Porphyra*, *Gigartina* and *Laurencia* appear above M.L.W.S. under conditions of extreme exposure indicates that these are extremely tolerant both of the actual force of wave shock and of the frequency of this factor.

Fauna

Barnacles. Three species of Cirripedes are considered, *Balanus perforatus* Brug., *Balanus balanoides* (L.), and *Chthamalus stellatus* (Poli). The last two thrive best at exposed points, and constitute the 'Balanoid zone' characteristic of such localities; *Balanus perforatus* is commonly found under rather more sheltered conditions and will be considered later.

Fischer-Piette (1933) and Moore & Kitching (1939) describe the distributions of *Balanus balanoides* and *Chthamalus stellatus* along British coasts; and it appears that Plymouth lies in an intermediate position on the south coast. Further west, towards Cornwall, *Balanus* dies out until *Chthamalus* only is left; further east, towards the Isle of Wight, it is *Balanus* which becomes increasingly dominant, and *Chthamalus* eventually disappears. In the Plymouth neighbourhood, however, both species occur freely, *Chthamalus* being dominant on the upper beach and *Balanus* on the lower beach. The effect of surf on the state of development of the Balanoid zone, and the negative correlation with fucoids have already been considered in this paper; various other general features are discussed in the work on Cardigan Bay, and here it is necessary only to consider the features of vertical distribution of the two species.

The upper limit of barnacles in quantity, or the '*Chthamalus*-line', usually best marked on steep exposed surfaces, varies in height in relation to the intensity of surf experienced (see Fig. 6A), and so does the absolute upper limit of *Chthamalus*. The outer reefs of Church Reef are thickly encrusted with this barnacle to above E.H.W.S., which is a reflexion not only of the exposure to strong surf but also of the low position of these reefs on the shore: they receive splash on a rough day even from low tides. Elsewhere the upper limit of barnacles in quantity varies from just above M.H.W.S. (at Bolt Head [*1*], etc.) to just above M.H.W.N. (e.g. on sheltered north faces at Jennycliff [*24*]). When shelter increases still further no distinct line can be recognized, and barnacles are reduced over the whole beach.

The lower limit of the barnacle belt, too, is frequently marked as a line on exposed vertical faces, i.e. the '*Balanus*-line'. In general this is less well marked than the *Chthamalus*-line, and is distinct only on steep faces at low-tide levels, but in places (e.g. at North Point), even when the rocks are horizontal, it is possible to recognize a fairly definite limit, below which barnacles in quantity die out. It is difficult to choose definite localities at which both the *Chthamalus*- and *Balanus*-lines are clearly recognizable, and at which the intensity of exposure is approximately equivalent at the top and the bottom of the shore, but an attempt is made to do this in Fig. 6A. It will be seen that, with increasing shelter, the lower limit of the Balanoid zone rises from M.L.W.S. to the region of M.L.W.N.; Fig. 6B gives a more comprehensive picture of this process. The same feature has been described in the Isle of Man by Moore (1935*a*). At many localities (e.g. North Point) it would appear that this raising of the lower level of the Balanoid zone is caused by the upward extension of the lower-shore fucoid belt, and this may be partially true. However, surf in itself also seems to have a more direct effect on the lower limit of barnacles in quantity. It is common to find protruding rocks near low-water level with a well-marked *Balanus*-line on their seaward face just above M.L.W.S., and with nothing below this line but a thin sheet of calcareous algae; obviously here

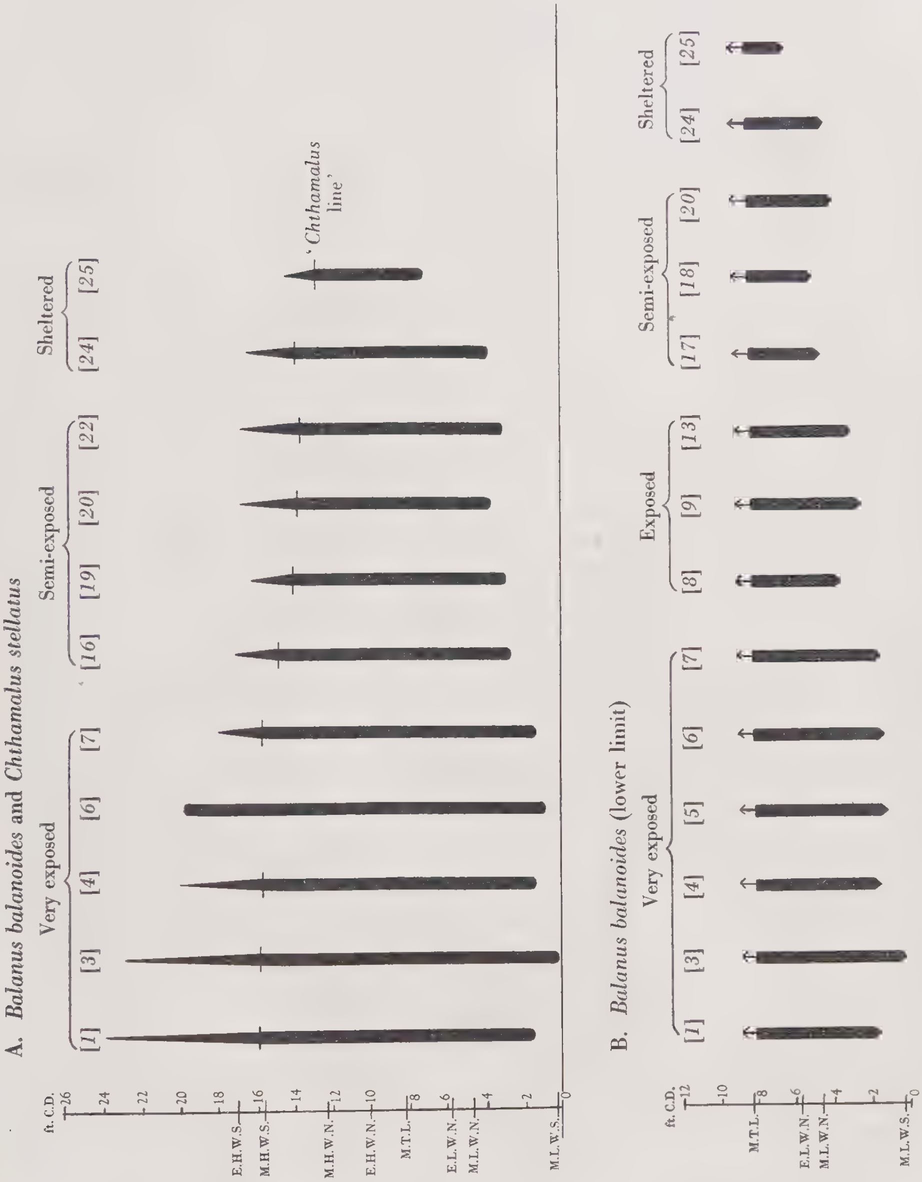

Fig. 6. Zonation of barnacles. (A) The vertical width of the Balanoid zone at different localities; (B) The lower limit of the Balanoid zone under different degrees of exposure to wave action.

fucoids are not limiting for the lower limit of *Balanus*. Moreover, on a similar vertical face to landward of the first (Fig. 7), there may be no fucoids again, but the *Balanus*-line is now no lower than M.L.W.N.; thus there appears to be a direct correlation between the intensity of surf and the lower limit of the barnacle zone. Moore (1935 *a*) suggests that the lowering of this limit by surf is partially due, at least, to the increased aeration of the water to greater depths, by wave-crash and backwash.

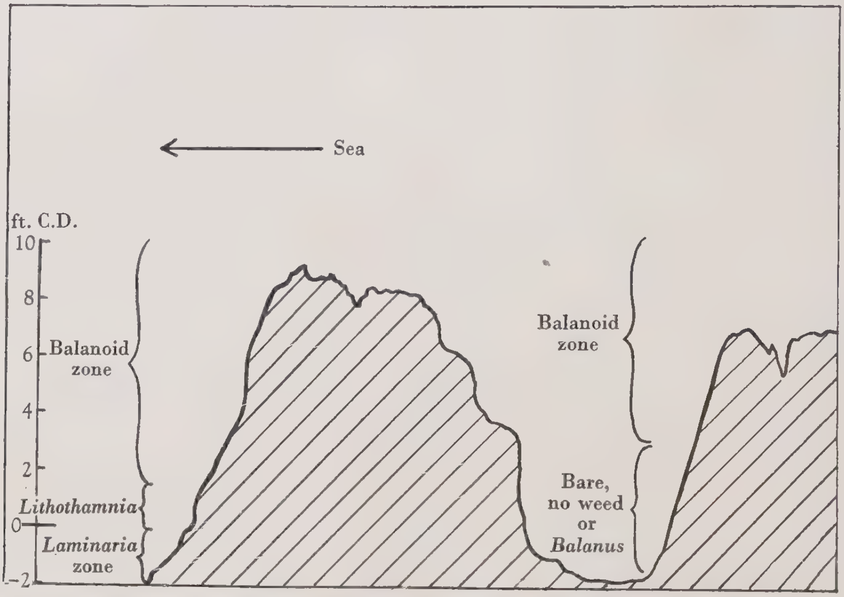

Fig. 7. Diagrammatic vertical section through reefs in Wembury Bay to show the effect of shelter on the lower limit of the Balanoid zone.

In the Balanoid zone *Chthamalus* is dominant on the upper shore, and *Balanus balanoides* lower down, but considerable overlapping of the zones of the two species occurs. Thus *Chthamalus* can persist as low as M.L.W.S. + 2 ft., and *Balanus* as high as M.H.W.N. or, when splash effects are introduced, as high as M.H.W.S. Generally speaking, however, M.L.W.N. is about the lower limit of *Chthamalus*, and M.H.W.N. is the upper limit of *Balanus balanoides*. In mid-beach then, there is a competition for space between the two species. From figures given by Moore (1935 *b*) it would appear that, in the Plymouth region, the transition from *Chthamalus*-dominance to *Balanus*-dominance takes place between M.T.L. and E.H.W.N. Without making a detailed analysis of the barnacle population at different points it is impossible to be certain, but the writer has gained the impression during this survey that the intensity of wave action may be a modifying factor in this respect. In Jennycliff Bay and on the north face of the Breakwater the transition occurs in the region of M.T.L., but on steep, exposed slopes at Bolt Head and Blackstone Point *Chthamalus* may be dominant as low as E.L.W.N.

Summarizing, then, intense wave action tends (*a*) to raise the upper limit of the Balanoid zone; (*b*) to lower the lower limit of the Balanoid zone; (*c*) possibly to lower the level at which the transition from *Chthamalus*-dominance to *Balanus*-dominance occurs.

Balanus perforatus Bruguière. Unlike the other two barnacles studied, this species is not overfond of strong surf, yet it favours a certain amount of water movement. Fischer-Piette (1936) has noted its scanty development on projecting headlands such as Start Point, and its improvement at wave-beaten positions in bays. It is obvious from the present survey, too, that *B. perforatus* is characteristic of semi-exposed situations; thus it was not found at Bolt Head or Blackstone, and is only occasional under extreme conditions of shelter (e.g. at Wilderness Point). In moderately exposed localities (e.g. Jennycliff Bay, Church Reef, North Point) the species is common in cracks, fissures, overhangs, etc., where surf is not too strong, and in such positions it may be the dominant barnacle over a small area of rock surface. On the flatter rocks on the west side of Queener Point, and on parts of the West Hoe rocks *B. perforatus* is very well represented and commonly associated with patches of *Mytilus edulis*. Mussels do not always occur where the barnacle is profuse, however, and the association, though frequent, is probably purely coincidental, as Fischer-Piette (1936) suggests.

Balanus perforatus extends to below M.L.W.S. in quantity, and its upper limit lies in the region of E.H.W.N.; though on north-facing overhangs on the outer reefs of Church Reef this may be raised by splash as high as M.H.W.N.

Littorina neritoides (L.). In the Plymouth locality, as in Cardigan Bay, this species is best represented on steep, rough, and very exposed surfaces, and is especially abundant at Bolt Head, Blackstone, and Queener Points. In semi-exposed localities (e.g. Jennycliff, Church Reef landward rocks, etc.), it is reduced in numbers; at North Point it is comparatively infrequent on the horizontal rocks; at Wilderness Point only very occasional specimens were found; while at Warren Point it was not taken at all. This agrees with the results of Lysaght (1941), who finds that *L. neritoides* is favoured by a barnacle-covered substratum but disfavoured by excessive development of weed. Both Lysaght (1941) and Colman (1933) discuss the tropic reactions of this snail, and Colman concludes that its restriction to cracks and crevices above high water is prompted by its need for shelter from wave shock. Yet, at Queener Point for example, it is common to find literally hundreds of individuals congregated on steep exposed surfaces in mid-beach, where the intensity and frequency of surf action are both high. It is probable that the adhesive powers of the snail are considerably stronger when it is wet than when it dries out, for *L. neritoides* above M.H.W.S. level can be easily blown off the rock.

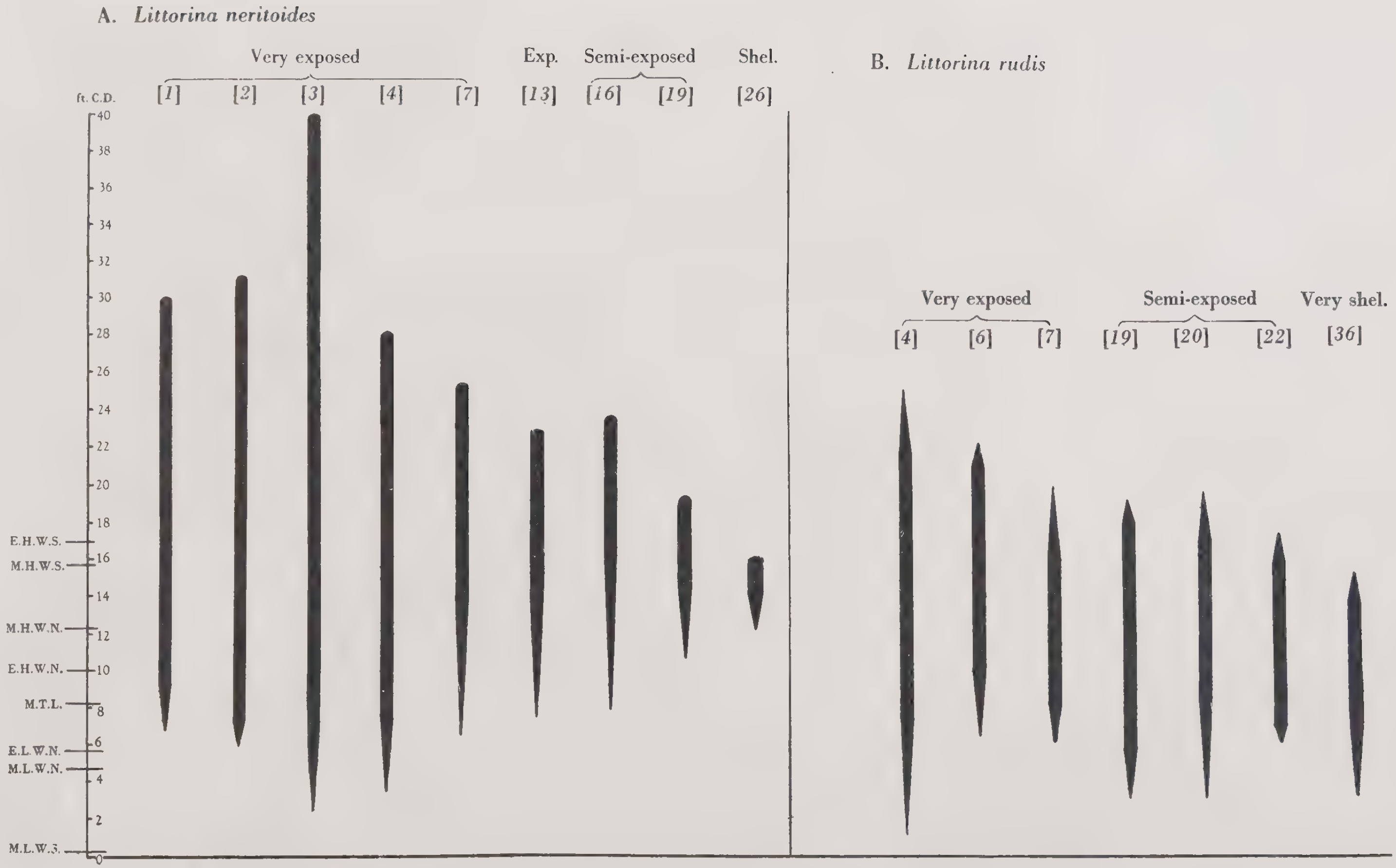

Fig. 8. Zonation of *Littorina neritoides* (A) and *L. rudis* (B).

The species is usually described as inhabiting levels above high-water mark, and, while it is admittedly most characteristic of such levels, occasional specimens were taken in Cardigan Bay as low as M.L.W.N. Lysaght (1941) records it to below M.T.L. on the Plymouth Breakwater, and reports the finding of mature snails on piles permanently submerged for at least a year. This being so, it is likely that Colman's (1933) lower limit, which he confesses is 'somewhat uncertain', is considerably too high. During the course of the present survey the species was definitely taken to below M.T.L. even on the landward portion of Church Reef, while at Blackstone Point it was found occasionally down to M.L.W.S. + 2 ft. (Fig. 8A). Although it was found to M.L.W.N. in Cardigan Bay, *L. neritoides* is never common much below M.H.W.S. in the region; in the Plymouth region, however, the writer has found dense congregations of the species in the M.T.L.-E.L.W.N. region (e.g. at Bolt Head, Reny, Blackstone, and Queener Points). Such groups are inevitably restricted to steep, rough faces, with a thick barnacle cover; on neighbouring flatter surfaces at the same shore level *L. neritoides* may be very occasional only. From Fig. 8A it can be seen that the intensity of surf raises the upper limit of distribution, and lowers the lower limit.

Littorina rudis (Maton). This species favours less exposed situations than *L. neritoides*, and is generally inferior to it in numbers at places such as Bolt Head, Blackstone, and Reny Rocks. On barnacle-covered slopes, *L. rudis* is largely confined to the shelter of empty barnacle shells. At North Point, Jennycliff Bay, Wilderness Point, and other semi-exposed or sheltered localities the species is more frequent than *L. neritoides*, occurring in large numbers among the sparse zones of *Pelvetia* and *Fucus spiralis* and at heights above these; but at Warren Point it is most abundant on shingle and boulders, and does not appear to favour the thick weed cover met with here. *Littorina rudis* is fond of somewhat irregular and broken rock, with plenty of pools, cracks, crevices, etc., while boulder areas (e.g. at Sandhill Point in the Salcombe Estuary) are usually well colonized by the snail. Vertical surfaces, unless deeply fissured and not exposed to excessive wave action, are not generally as popular as more level rock.

The upper limit (Fig. 8B) is lower than that of *L. neritoides* but may be raised by splash. The species is usually not very common much below M.T.L., and the intensity of surf does not appear to have any marked modifying effect on the lower limit of distribution. On the Breakwater, *L. rudis* was not taken below E.L.W.N., but on Queener Point specimens were found as low as M.L.W.S. + 1 ft.; Moore (1940) also describes the lower limit of this species as variable.

Littorina littorea (L.). This is even less tolerant of surf than *L. rudis*, and no specimens were recorded at Bolt Head, Reny, Blackstone, or the Breakwater, while at Queener Point it is occasional only in sheltered gulleys. At North Point, and in Jennycliff and Wembury Bays it occurs very commonly on level broken ground where weed is not too profuse. In the Yealm estuary *L. littorea* is abundant on the stony beach in the neighbourhood of Warren Point, and may be the dominant animal species on such a substratum. Its habit of congregating on boulders, on isolated weed clumps, in shallow pools, etc., is well marked, and leads to a somewhat local distribution. Curiously, *L. littorea* was not found, even in local shelter or on suitable ground, in the Tinside-West Hoe region, and was only occasionally recorded at Wilderness Point, both of which are limestone areas.

The upper limit of distribution (Fig. 9A) is variable, and appears to be raised by splash. The lower limit is not well defined either; the snail generally occurs lower on stones (e.g. at Warren Point) and in gulleys than it does when the lower shore is densely covered by fucoids. It is most abundant above M.L.W.S. + 2 ft., but at Warren Point [*36*] it is common as low as M.L.W.S. − 0·5 ft.

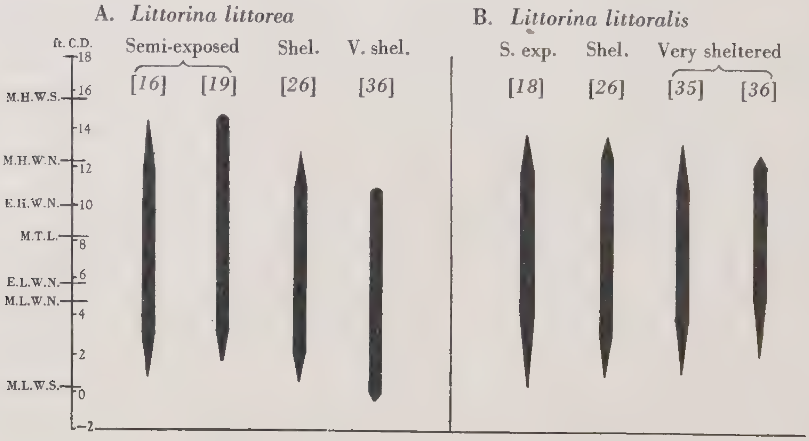

Fig. 9. Zonation of *Littorina littorea* (A) and *L. littoralis* (B).

Littorina littoralis (L.). As usual, *L. littoralis* is confined to fucoid areas, and was found to be most abundant in weed zones at Church Reef, Wilderness Point, Warren Point, and Jennycliff. Yet at Fort Charles west, where the *Fucus vesiculosus* belt is good, *Littorina littoralis* is surprisingly poorly represented. In its vertical distribution, too, *L. littoralis* is influenced by the distribution of fucoids. Thus the scarcity of weed on the stony lower beach at Warren Point (Fig. 9B [*36*]) results in the occasional presence of the snail. Generally speaking the zone of abundance of *L. littorea* lies between M.H.W.N. and M.L.W.N. (Fig. 9B), but occasional specimens have been taken as high as M.H.W.N. + 1 ft. and as low as M.L.W.S. In moderately exposed and sheltered localities (e.g. Jennycliff Bay and Warren Point) *L. littoralis* occupies a somewhat higher zone on the beach than *L. littorea.*

Osilinus lineatus (da Costa). *Osilinus* is intolerant of excessive exposure to surf, and was not found at Bolt Head, Blackstone, on the south face of the Breakwater, or on the outer reefs of Church Reef. At Queener Point the species is entirely confined to the shelter of gulleys and channels. It was not taken at Tinside, and only a single specimen was discovered, after prolonged search, at Wilderness Point; Moore (1940) also records its absence from Rum Bay, which is another limestone area, yet on the Staddon Grits of Jennycliff Bay, a short distance away, *Osilinus* is quite common. The favourite habitat of the species is the same as it is in Cardigan Bay, i.e. fairly sheltered level rock, or areas of boulders and shingle, especially when these occur in gulleys. On such ground the snail is common in Jennycliff Bay, and very frequent along the shore of Wembury Bay to Church Reef. On Church Reef, it is local in distribution on the landward portion, but is not as restricted in its horizontal distribution as Colman (1933) describes. At Warren Point, though *Osilinus* does occur under weed, it is much more abundant on shingle areas, and an '*Osilinus* zone' may be recognized at the top of the stony beach here, as in many places in Cardigan Bay. On steep faces, when these are very sheltered, the snail is occasional, but it was never found on overhanging surfaces.

Colman (1933) describes a very narrow vertical range for *Osilinus*, between M.H.W.N. and E.H.W.N. In Cardigan Bay the species has been found to occupy a much wider range, from above M.H.W.N. to M.L.W.N., while Moore (1940) has described a similar range at Wembury. Fig. 10B shows that its general zonation lies between high and low water neaps at the four localities at which it occurs in numbers. It would appear that here, again, splash is effective in extending the upper limit. The low lower limit at Warren Point [*36*] may be due to the stony lower beach, which is an ideal habitat for *Osilinus*. Above E.H.W.N. the snail is frequent on open rock surfaces, below this level it is confined to gulleys, though not necessarily to gulleys with a fresh-water influence as Walton (1915) suggests. Possibly this restriction of the species to gulleys at levels below E.H.W.N. may be due to the frequency of wave shock at such levels.

Gibbula umbilicalis (da Costa). At Bolt Head, Blackstone and Reny, *G. umbilicalis* is confined to pools and crevices; and while it is intolerant of excessive surf action, it is rather more tolerant of this factor than *Osilinus* or *Littorina littorea*. However, it favours similar ground to the last two species, i.e. flat, fairly sheltered rocks, boulders and stones, etc., though it is more commonly associated with fucoids than is *Osilinus*. Lithothamnia-encrusted pools often contain a few *Gibbula umbilicalis*, and on exposed points the species may be entirely restricted to such pools. This species, again, is poor on the limestone of Wilderness Point, and very occasional from Tinside to West Hoe. Yet it is fairly common on the limestone blocks of the Breakwater and in the holes and cracks between these blocks.

G. umbilicalis is slightly lower in its vertical distribution than *Osilinus* (see Fig. 10C); its upper limit lies generally between E.H.W.N. and M.H.W.N., but may be raised by splash. In the M.L.W.N.-M.L.W.S. region the species tends to die out in numbers, but it may often be found as low as M.L.W.S., or slightly lower than this.

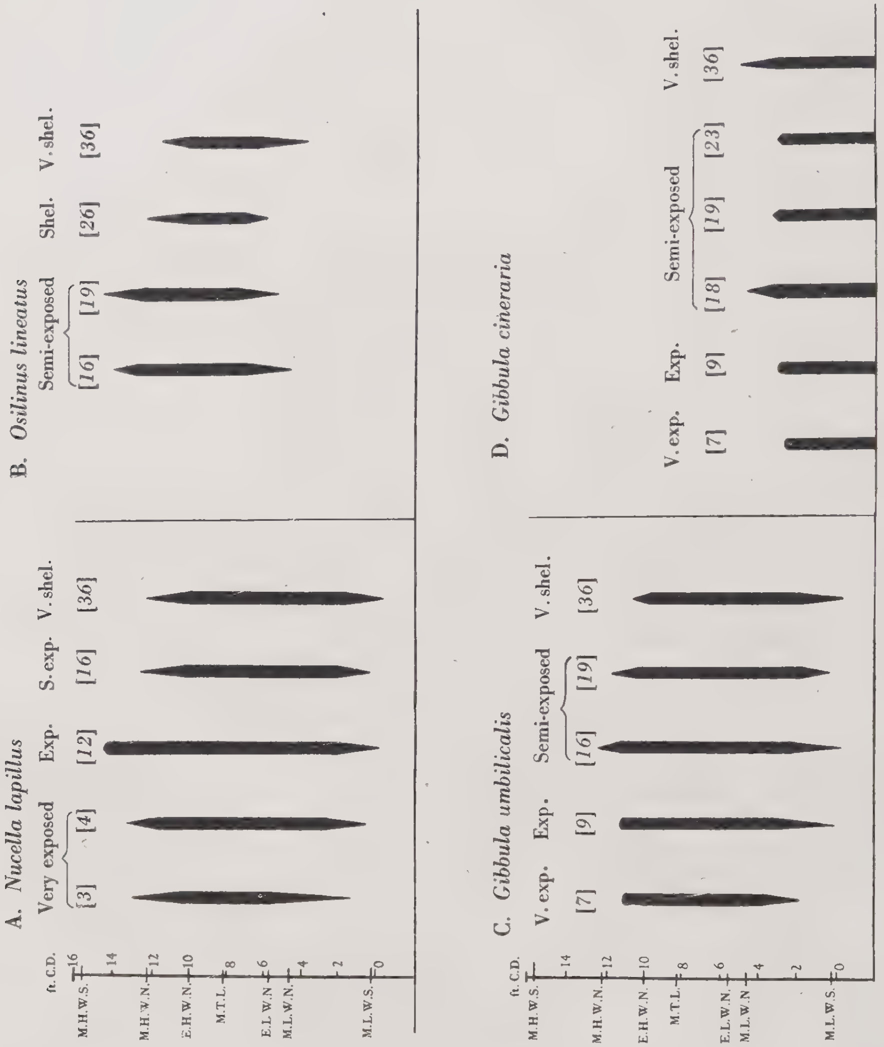

Fig. 10. Zonations of *Nucella lapillus* (A), *Osilinus lineatus* (B), *Gibbula umbilicalis* (C) and upper limit of *G. cineraria* (D).

Gibbula cineraria (L.). This is absent or extremely rare at exposed points such as Bolt Head, Blackstone, Reny, and Queener Point, but may be fairly common in more sheltered localities, with the exception of Tinside and Wilderness Point. Its favourite habitat is stony gulleys near low-water mark, where it commonly occurs under the stones. Specimens have also been taken on rock under weed, e.g. in the Laminarian zone at Fort Charles, and in the *Himanthalia* zone on the Breakwater.

From the sublittoral *Gibbula cineraria* extends up to about 3 ft. above C.D., while occasionally it was found to M.L.W.N. Except for a single specimen found in a crack as high as 6 ft. above C.D., on the south face of the Breakwater, the species was not recorded above M.L.W.N. anywhere (Fig. 10D).

Nucella lapillus (L.). *Nucella*, though it is not tolerant of heavy surf, may be quite common even on exposed headlands provided local shelter is available; thus at Blackstone Point the snail is present in appreciable numbers in the deep crevices between the steep ridges of slate. Yet, at North Point, where surf action is considerably less intense than it is at Blackstone, the species is not at all common; presumably this is due to the smoother contours of the rock and the absence of deep cracks and fissures in the felsite strata. Normally *Nucella* is not over-fond of a thick cover of weed (e.g. at Warren Point), possibly because of the paucity of barnacles (one of its main articles of diet) in such areas, yet at North Point it is curious to find a larger number of the snails under clumps of weed than on neighbouring bare rock. It appears that the shelter afforded by weed, on such a level beach as North Point, may be important. Except in sheltered conditions *Nucella* is not favoured by steep or vertical faces, but is frequently found in groups on such faces when they face away from the sea; and as the writer has already suggested in Cardigan Bay, there is some indication that, at the top of its distribution, *Nucella* may seek such surfaces partly at least because of their shade. This species, again, is poor on the Tinside-West Hoe limestone rocks and on Wilderness Point, though in the latter case the paucity of barnacles may be partially responsible. It is not particularly well represented in Jennycliff Bay either, though barnacles and local shelter are both available here.

The vertical zonation of *Nucella* is depicted in Fig. 10A. The upper limit of the species in quantity lies between E.H.W.N. and M.H.W.N. at most places, but in cracks and fissures on the landward faces of the low-tide reefs at Wembury [*12*] it occurs up to between M.H.W.N. and M.H.W.S. in numbers. At Warren Point [*36*], with decreased splash, *Nucella* is common as high as E.H.W.N. only, but even here it is occasional to M.H.W.N. The lower level of abundance lies in the M.L.W.N.-M.L.W.S. region, except at Blackstone Point [*3*]; here the rock configuration changes in the neighbourhood of E.L.W.N., and below this level local shelter (crevices, etc.) is infrequent, so that *Nucella* too is infrequent. Moore (1938) states that *Nucella* extends to below low water, and it has been definitely recorded to below M.L.W.S. at Church Reef and Warren Point. Comparing Figs. 10A and 6A it will be noted that the zone of abundance of the gastropod lies, in all instances, within the Balanoid zone.

Patella vulgata L. One of the most ubiquitous animals on the shore, this species ranges from conditions of extreme exposure to those of extreme shelter from surf. Yet it does not particularly favour the thick weed zones of sheltered localities, and where weed is profuse limpets are generally most numerous on bare protruding peaks and ledges. Hatton (1938) describes a denser settling of *Patella* on exposed faces than on sheltered ones, and it is possible that the filtering effect of the algal fronds is important in this respect during the time of settling. Moreover, where weed is thick (e.g. at Wilderness Point), the underlying rock is frequently coated with a layer of silt, smaller algae, sponges, and hydroids, forming a dense mat. Such a substratum is shunned by *Patella*, which is restricted to areas of barer rock. On very wave-beaten slopes (e.g. the seaward peaks of Church Reef), the competition between *Patella* and barnacles for space is often very noticeable. Where barnacles extend over practically the whole of the available space (even over the limpet shells themselves) *Patella* is almost invariably represented by small individuals only; larger shells are found only where barnacles are less dense. This, too, is commented upon by Hatton (1938) who, in addition, has observed a denser settling of limpet larvae on bare or artificially-denuded surfaces, than on those thickly covered with barnacles. The same worker describes experiments which demonstrate that the size of *Patella* is limited by the density of the surrounding barnacle population. With regard to rock slope and texture, *P. vulgata* is very tolerant; it occurs on the roughest rocks and on smooth pebbles; it is frequent on all angles of slope, including overhangs, and may even exist on very small stones where these are not subject to much movement (e.g. at Warren Point).

P. vulgata definitely persists to below M.L.W.S., but does not appear to reach E.L.W.S.; however, it occurs lower than the lower limit of 2 ft. above C.D. described for it by Colman (1933). Just above M.L.W.S. there is some evidence of its dying out in numbers, and *Patella athletica* becomes the dominant limpet on exposed rocks at such levels. With regard to the upper limit of *P. vulgata*, Orton (1929) considers that the orientation of the rock surface, the height of splash, the latitude of the locality, and the epoch of the day at which low springs occurs, are all important. Within the geographical limits of the present survey the last two factors are constant, and variations in the upper limit of the species can be ascribed to variations in the first two influences. It is often difficult to disentangle these two effects, for usually south-facing surfaces receive both maximum splash and maximum illumination, one factor tending to raise, the other to lower, the upper limit of distribution. In Fig. 11 is presented a selection of data arranged to illustrate the effects both of splash and shade. On south faces at Warren Point [*36*], on sheltered south faces at Jennycliff, and on similar rocks in Wembury Bay [*32*], *P. vulgata* occurs only to just below M.H.W.N. in the open, and is common only from E.H.W.N. down. These localities are represented in the centre of the text-figure. Proceeding to the left of this figure, all the localities are south-facing, and the illumination factor is therefore constant. Exposure to wave action, and the amount and height of splash are increasing, however, and it is obvious that the upper limit of *P. vulgata* is rising, until, on the seaward reefs of Church Reef [*6*], the

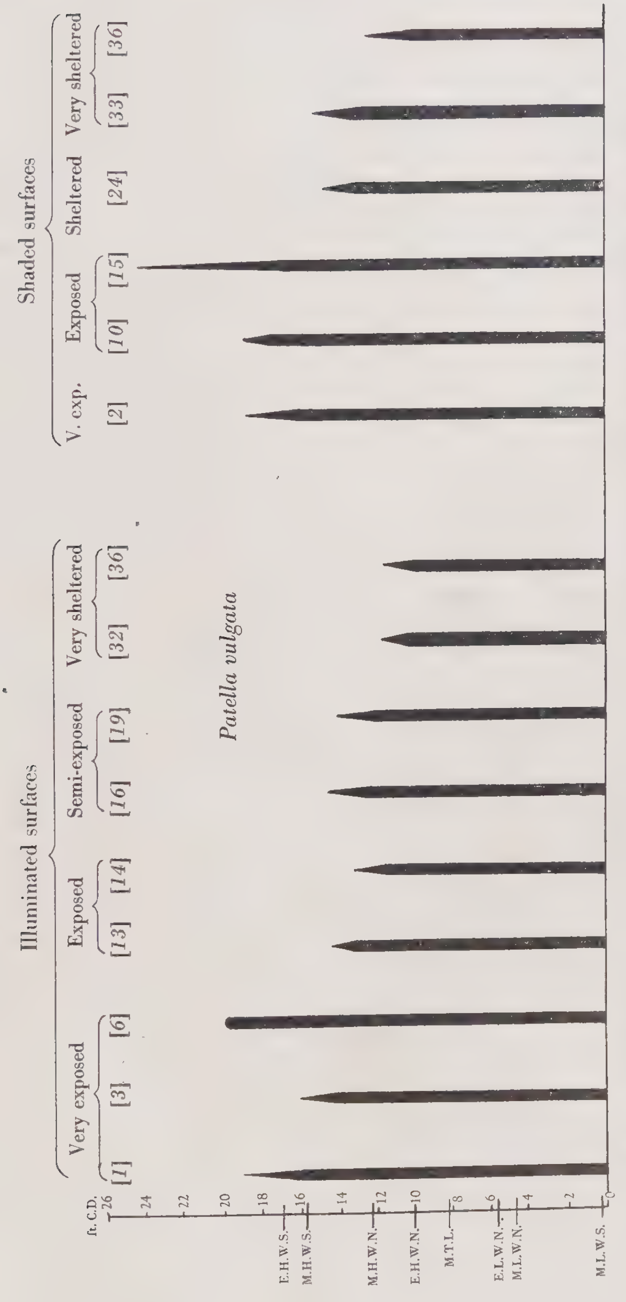

Fig. 11. Variations in the upper limit of distribution of *Patella vulgata* under different conditions of exposure to wave action and illumination.

species is common to above E.H.W.S. This is the effect of splash on fully illuminated surfaces. On the right-hand side of the figure surf action and splash are again decreasing from left to right but at all these localities *P. vulgata* is either situated on a shady aspect or is covered by weed. Here again the upper limit is influenced by splash. The effect of shade may be seen by comparing illuminated and shady surfaces at the same locality. Column [*3*] in Fig. 11 represents the zonation on a south-east-facing rock at Blackstone Point, i.e. a surface receiving both maximum sunlight and maximum wave action; column [*10*] the zonation on the north-west, and therefore shaded and sheltered, face of the same peak. *P. vulgata* extends almost 4 ft. higher on this north-west face, i.e. the absence of splash is more than compensated for by the reduction in illumination. The highest record of *P. vulgata* made during the survey was in a narrow vertical shaft or 'blow-hole' in Wembury Bay [*15*]; water rushes through this with considerable force, and splash is experienced to great heights, moreover the sides of the shaft are almost perpetually shaded, and limpets were found here as high as 8 ft. above E.H.W.S. Generally speaking, then, the upper limit of *P. vulgata* in the Plymouth neighbourhood, lies in the region of M.H.W.N., but it is liable to be raised by shade, weed-cover, and splash.

Patella depressa Pennant. This limpet, though commonly taken during the survey, is less tolerant of sheltered conditions than *P. vulgata*, and is best represented at Bolt Head, Reny, Blackstone Point, Queener Point, and on the outer reefs of Church Reef. In semi-exposed localities such as Jennycliff, North Point, etc., it is more restricted in its distribution, occurring locally on vertical, exposed rock faces. At Wilderness and Warren Points it was not recorded. Fischer-Piette (1935) also remarks on its need for exposure to surf.

The species occupies much the same levels (Fig. 12A) in the Plymouth locality as it was found to occupy in Cardigan Bay; it extends up to M.H.W.N. on the Breakwater's south face [7], at Tinside, and in Jennycliff Bay, but at Bolt Head [*1*] this upper limit is raised by splash to E.H.W.S. The lower limit is vague, *P. depressa* does not extend below M.L.W.S. anywhere, and it dies out in numbers between M.L.W.S. and M.L.W.N. in most places. On the south face of the Breakwater [7] it is only occasional from E.L.W.N. down, as the protective blocks in front tend to exercise some sheltering influence on the lower part of this slope. As usual *P. depressa* is a common inhabitant of lithothamnia-encrusted pools at exposed points, and in such pools it may be common to above E.H.W.S.

Patella athletica Bean. This species, too, is best on wave-beaten reefs and headlands, and was not taken at either Warren or Wilderness Points. However, it is rather more frequent than *P. depressa* at Fort Charles; moreover, it is generally found on less steep rocks than the other, giving the impression that here, as in Cardigan Bay, it is somewhat less demanding of surf than *P. depressa*. Fischer-Piette (1935) is inclined to adopt the opposite view.

P. athletica is characteristic of exposed reefs on the lower shore, where fucoids are poor or absent and *Corallina* is the chief alga, but it has also been found in shaded overhangs. In lithothamnia-encrusted pools it is common to above high water, and in such pools it is usually more frequent than either *Patella vulgata* or *P. depressa*.

Whenever it occurs, *P. athletica* is common down to the lowest level examined. The upper limit (Fig. 12B) is again affected both by splash and shade; on very exposed surfaces it may reach almost to M.T.L., on more sheltered reefs it extends as high as M.L.W.N. only, while under overhangs it was occasionally taken above M.T.L. as in Cardigan Bay.

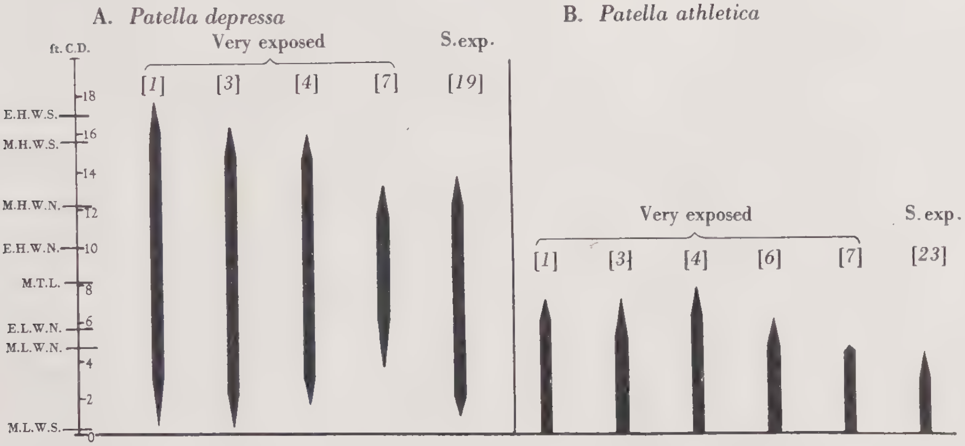

Fig. 12. Zonation of *Patella depressa* (A) and upper limit of *P. athletica* (B).

Discussion on the Distribution of the Fauna

It has been shown that, for algae, surf acts chiefly, (*a*) as a presence or absence factor, and (*b*) as a modifying influence on the extent and position of algal zones. Much the same is true with regard to the fauna:

(1) As a presence or absence factor, wave action determines the density of the population of *Chthamalus*, *Balanus balanoides*, *Littorina neritoides*, *Nucella lapillus*, *Patella vulgata*, *P. athletica*, all of which species favour somewhat exposed conditions. The effect of surf on such animals may be directly concerned with transport of food, larvae, oxygen, etc. (as is probably true for barnacles); or it may be concerned in that it determines the height and frequency of splash and spray (e.g. for *Littorina neritoides*). With *Patella vulgata*, Hatton's (1938) experiments have shown that heavy surf favours a denser settling of larvae; the same is probably true for *P. depressa* and *P. athletica*, though for these two limpets there appears to be an additional effect restricting them to exposed localities. The nature of this influence is unknown.

For *Nucella* the effect of surf is indirect, in that it provides an abundant barnacle population which the gastropod can utilize for food; for barnacles themselves, too, surf has an indirect as well as a direct effect, in that it tends to remove algal competition. For *Littorina littoralis* this effect is reversed, i.e. surf, by discouraging fucoids, also discourages the snail. The adverse influence of excessive wave action on free-living gastropods such as *Osilinus*, *Littorina littorea* and *Gibbula* is, in all probability, a purely mechanical one, tending to knock such animals off the rock and damage their shells.

(2) As a modifying factor on vertical zonation, exposure to surf raises the upper limits of *Balanus balanoides*, *B. perforatus*, *Chthamalus stellatus*, *Littorina neritoides*, *L. rudis*, *L. littorea*, *Osilinus*, *Gibbula*, *Patella vulgata*, *P. depressa* and *P. athletica*. It also lowers the lower limit of *Balanus balanoides* (probably a direct effect in increasing the oxygenation), of *Nucella* (an indirect effect correlated with the lowering of the barnacle limits) and of *Littorina neritoides*. In addition, there is a possibility that surf may have some influence on the level of the *Chthamalus-Balanus* transition.

(3) Furthermore, intense surf action may impose a limit on the size of individuals. Thus, on exposed slopes, *Littorina rudis* is represented by small individuals only, small enough to shelter in empty barnacle shells, i.e. a direct effect. With regard to *Patella* on exposed slopes, its reduction in size is an indirect reflexion of the influence of surf on the density of the barnacle population.

General Discussion

The relation of intertidal species to percentage exposure to the air

The figures of Colman (1933, table VI, p. 456) for percentage exposure to the air at different shore levels are here taken as applicable; these are based on the 1930 tides, but are not likely to vary greatly from year to year. For comparison with Cardigan Bay I have chosen the landward portion of Church Reef. This locality represents intermediate conditions between the extreme exposure of Bolt Head and Blackstone Point, for instance, and the extreme shelter of Warren and Wilderness Points; as nearly as can be judged, the exposure to surf here is roughly equivalent to that experienced on the Cardiganshire coast; moreover, the results can be compared with those of Colman (1933). Fig. 13 summarizes the zonation of the various species studied on Church Reef, with the percentage-exposure curve superimposed. Table III compares the percentage-exposure limits of the species: (1) on Church Reef (present survey); (2) on Church Reef (according to Colman, 1933)—again the 'splash allowance' has been deducted, and the figures are based on Colman's 'extreme values' (1933, p. 454, tables IV and V); (3) in Cardigan Bay. In addition, (4) the extreme limits to which the species were found anywhere during the South Devon survey are also figured.

Comparing columns (1) and (2), the advantage of a wide-scale survey over a detailed but local traverse survey is obvious; for practically all the species, excepting *Fucus serratus*, *Littorina littorea*, *L. littoralis*, and *Gibbula cineraria*, were found to have a wider distribution on Church Reef than appeared from Colman's traverses. *Fucus serratus* and the two species of *Littorina* are similarly zoned by both surveys, but *Gibbula cineraria* was recorded much higher by Colman than by the present worker; and the same is true of the upper limit of *Lichina pygmaea*.

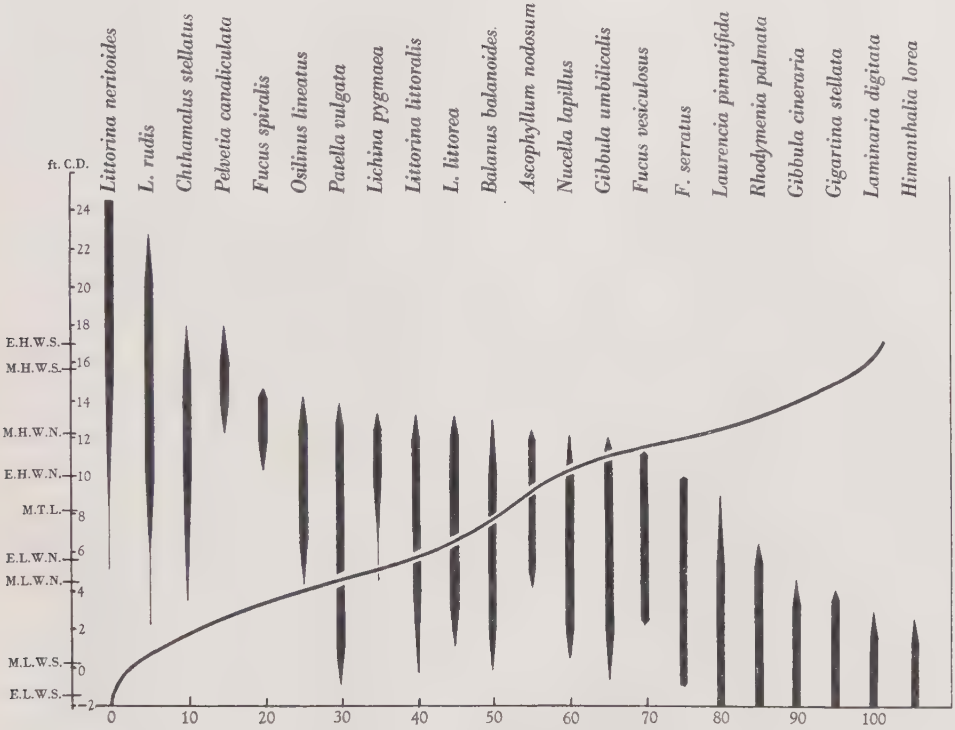

Fig. 13. Zonation of species on the landward portion of Church Reef, Wembury. The curve representing the percentage exposure to the air at different tidal levels is superimposed.

It appears, from a comparison of columns (1) and (4) that, with few exceptions, the plants and animals on Church Reef do not occupy the whole ranges possible to them. Here, however, the factor of exposure to wave action and splash is introduced, and it is obvious that at places like Bolt Head the vertical ranges are widened by this factor.

Comparing columns (3) and (4) it will be seen that, generally speaking, there is a fair degree of similarity between the zonation of littoral species in the

TABLE III. PERCENTAGE EXPOSURE TO THE AIR OF SPECIES IN CARDIGAN BAY, ON CHURCH REEF, AND IN THE PLYMOUTH NEIGHBOURHOOD

	(1) Church Reef (1946)		(2) Church Reef (Colman)		(3) Cardigan Bay		(4) Plymouth neighbourhood	
Species	Upper limit (%)	Lower limit (%)	Upper limit (%)	Lower limit (%)	Upper limit (%)	Lower limit (%)	Upper limit (%)	Lower limit (%)
Ascophyllum nodosum	77	25	75	30	71	15	83	10
Balanus balanoides	83	3	80	5	83	0	96	0
Chthamalus stellatus	100	17	100	20	100	28	100	10
Fucus serratus	58	0	60	0	56	0	58	0
F. spiralis	93	60	90	70	96	55	94	56
F. vesiculosus	69	16	—	—	63	8	83	5
Gibbula cineraria	29	0	40	0	21	0	33	0
G. umbilicalis	76	0	65	5	63	2	76	0
Gigartina stellata	25	0	20	0	26	0	39	0
Himanthalia lorea	15	0	—	—	—	—	41	0
Laminaria digitata	18	0	12	0	20	0	25	0
Laurencia pinnatifida	54	0	—	—	60	0	56	0
Lichina pygmaea	87	30	97	52	100	22	100	33
Littorina littoralis	85	2	87	7	81	4	85	2
L. littorea	83	6	85	8	71	7	93	1
L. neritoides	100	38	100	90	100	20	100	13
L. rudis	100	12	100	60	100	8	100	7
Nucella lapillus	76	4	65	8	62	0	93	0
Osilinus lineatus	90	30	75	60	82	22	93	24
Patella athletica	—	—	—	—	42	0	45	0
P. depressa	—	—	—	—	92	0	100	0
P. vulgata	98	0	98	12	100	0	100	0
Pelvetia canaliculata	100	85	98	86	100	87	100	65
Rhodymenia palmata	44	0	—	—	35	0	47	0

Plymouth neighbourhood and in Cardigan Bay. The following exceptions are worth noting:

(*a*) *Pelvetia* appears to be able to exist at lower levels in South Devon, but only at Wilderness and Warren Points of the localities investigated in the present survey (see Fig. 3A). It seems probable that its lower limit in Cardigan Bay and at exposed or semi-exposed localities near Plymouth is raised by surf (i.e. the combined effects of strength of wave shock and frequency of wave shock) as already described. Conditions as sheltered as those at Wilderness and Warren Points are not met with anywhere on the part of the Cardiganshire coast investigated. Moreover, the effect of splash in raising the effective height of tides is important; thus the level of M.H.W.N. at Bolt Head may be almost as damp as E.H.W.N. at Warren Point, and if the lower limit of *Pelvetia* is determined by some ill-effect of immersion then the effective (as opposed to the predicted) height of tides will be important. At Church Reef, it should be noted, the lower limit of the alga is very similar to that in Cardigan Bay, and here surf effects are more or less equivalent.

(*b*) The algae *Rhodymenia*, *Gigartina* and, to a lesser extent, *Laminaria digitata*; the barnacle *Balanus balanoides*, and the limpets *Patella depressa* and

P. athletica, all have higher upper limits in the Plymouth neighbourhood than they do in Cardigan Bay. *Littorina neritoides* and *Ascophyllum* have lower lower limits. Yet, comparing the semi-exposed locality of Church Reef with the coast of West Wales, the discrepancies are less marked. It has already been shown that surf exerts an elevating effect on such upper limits (and a depressing effect on the lower limit of *Littorina neritoides*), and the differences are probably due to the extreme exposure to surf encountered at Bolt Head, Blackstone, etc., which is unparalleled anywhere in Cardigan Bay. The same is possibly true with regard to the upper limits of *Fucus vesiculosus* and *Ascophyllum*. While these are only able to tolerate a certain maximum of surf, which is often exceeded in Cardigan Bay, it is possible to discover their existence in local shelter (fissures, etc.) at exposed points near Plymouth, where they receive more splash, and their environment is considerably damper, than it is anywhere on the Cardiganshire coast, at an equivalent level.

(*c*) The lower limit of *Chthamalus* is interesting. Moore & Kitching (1939) describe how, proceeding eastward along the south coast, and northwards along the west coast of Britain, this barnacle not only tends to die out in numbers, but becomes less tolerant of conditions on the lower beach. This, these workers suggest, is due to the fact that, as certain factors (lack of Atlantic water?) become critical for the barnacle, it becomes less tolerant of the ill-effects of immersion. This explains the difference in lower level of *Chthamalus* in Cardigan Bay from that in the Plymouth neighbourhood.

Apart from these exceptions, the zonations of *Fucus spiralis*, *F. serratus*, *Laurencia pinnatifida*, *Littorina rudis*, *L. littoralis* and *Patella vulgata*, are very similar in both localities. Thus, out of twenty-two species common to the two surveys, no fewer than sixteen are either similar in their zonation at both places or the differences can be explained by the known facts of surf effects, while the differences for *Chthamalus* are also explicable. The exceptions are: *Osilinus*, *Nucella*, *Gibbula umbilicalis*, *G. cineraria* and *Littorina littorea*. All these appear to be somewhat more tolerant of exposure to the air in the Plymouth neighbourhood than they are in West Wales, and since the differences in the upper limits of these species are also manifested under the semi-exposed (to surf) conditions of Church Reef, splash effects can hardly be held to account for this. No satisfactory explanation or suggestion can, as yet, be put forward.

Critical Levels

Certain levels have been shown (Evans, 1947) to be more critical than others in connexion with the distribution of intertidal plants and animals in Cardigan Bay. These are:

(1) Between M.L.W.S. and E.L.W.S., where the majority of intertidal species achieve their lower limits.

(2) Between M.L.W.S. and M.L.W.N., which marks the lower limits of certain other intertidal species.

(3) Just above M.L.W.N., where several sublittoral species reach their upper limits of penetration into the intertidal zone.

(4) Just below M.H.W.N., marking the upper limit of one set of intertidal species.

(5) Between M.H.W.S. and E.H.W.S., where a further set of intertidal plants and animals achieve their upper limits.

These were compared with levels described by Colman (1933) as critical for a similar set of species on Church Reef, and the points of difference were discussed. During the present work the writer has attempted to recognize such levels, not only on Church Reef, but also at the other localities studied. However, at many stations (e.g. Bolt Head, Blackstone, Reny, etc.) so many species are unrepresented or occur very infrequently that such localities are best omitted from the discussion. Sufficient data are available for North Point, Queener Point, Jennycliff Bay, and Wilderness Point, and since these display a fair range in conditions of shelter and exposure to surf, the discussion will be based on these. The method used by Colman (1933, p. 463) to elucidate critical levels has been followed, i.e. the number of upper and lower limits occurring between −2 ft. and +1 ft. C.D., between −1 ft. and +2 ft. C.D., between 0 and +3 ft. C.D., etc., was calculated for each station. Graphs were drawn in the way that Colman describes, and the peaks of such graphs were taken to mark critical levels. The results are summarized in Fig. 14; the brackets embrace the levels (e.g. +2 ft. and +6 ft. C.D.) between which the various maxima occur. The Cardigan Bay results are included in the same figure, also results achieved by interpreting Colman's (1933) data for Church Reef (without a splash allowance). The numbers (1) to (5) are equivalent at all localities.

It will be observed that levels (1) and (2), which are separate entities in Cardigan Bay, at Church Reef, North Point and Wilderness Point, are not distinguishable from each other at either Queener Point or Jennycliff; neither do they appear as separate levels from Colman's survey of Church Reef. At the first two localities in Fig. 14 (i.e. Cardigan Bay and Church Reef), these levels mark the lower limits of the following intertidal species.

LEVEL (1): *Patella vulgata*, *Balanus balanoides*, *Littorina littoralis*, *L. littorea*, *Gibbula umbilicalis*, *Nucella lapillus* and *Fucus serratus*.

LEVEL (2): *Littorina rudis*, *Chthamalus stellatus*, *Lichina pygmaea*, *Ascophyllum nodosum*, *Fucus vesiculosus*, and *Osilinus lineatus*. (In Cardigan Bay, *Littorina neritoides* also ends within this region, at Church Reef it ends slightly above it.)

At Queener Point there is a single maximum, marked on Fig. 14 as (1 and 2). Within the levels enclosed by this bracket all the species represented in levels (1) and (2) of Cardigan Bay achieve their lower limits, with the exception of *Littorina littorea*, *L. littoralis*, *Ascophyllum*, *Fucus serratus* and *Osilinus*, all of which are either totally absent from Queener Point or occur too infrequently to zone. Thus the merging of (1) and (2) into a single critical level at this locality is due to the lowering, by intense surf action, of the lower limits of *Chthamalus*, *Littorina rudis* and *L. neritoides*; so that the two separate critical levels cannot be distinguished, and there occurs a single maximum between −1 ft. and +3 ft. C.D.

At North Point we appear to have what is an intermediate stage between Cardigan Bay and Queener Point. Here, (1) and (2) overlap; again due to the depression of the lower limits of *Chthamalus* and *Littorina rudis*, and also of *Osilinus*; but *Littorina neritoides* achieves its lower limit higher up.

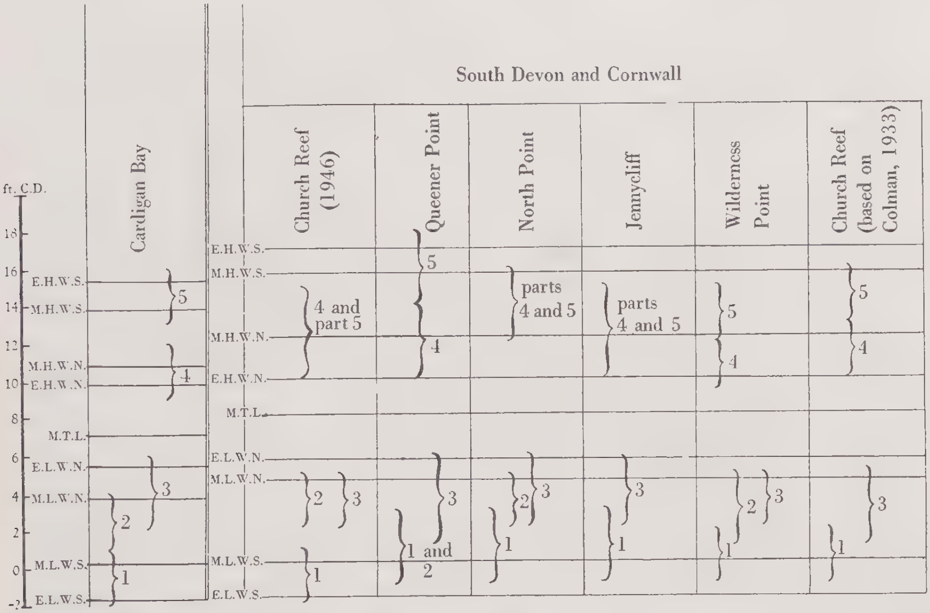
ft. C.D.
18
16
14
12
10
8
6
4
2
0
-2
E.H.W.S.
M.H.W.S.
M.H.W.N.
E.H.W.N.
M.T.L.
E.L.W.N.
M.L.W.N.
M.L.W.S.
E.L.W.S.
Cardigan Bay
South Devon and Cornwall
Church Reef (1946)
Queener Point
North Point
Jennycliff
Wilderness Point
Church Reef (based on Colman, 1933)
5
4
3
2
1
4 and part 5
1 and 2
parts 4 and 5

Fig. 14. The position of 'critical levels' in Cardigan Bay and in localities in South Devon and Cornwall. For explanation, see text.

From the four examples: Cardigan Bay, Church Reef, North Point, and Queener Point, then, it would appear that heavy surf action, by permitting certain species to extend their lower limits of distribution, leads to the appearance of a single critical level marking the lower limit of intertidal species instead of two such levels.

In Jennycliff Bay, however, level (1) does not represent a combination of (1) and (2); here the lower limits of *Littorina rudis*, *L. neritoides*, and *Osilinus* are raised by shelter, *Lichina* is unrepresented. Moreover, though *Ascophyllum* and *Fucus vesiculosus* end in the M.L.W.N. region, the number of limits becomes spread out, and no clear maximum can be recognized except the one just above M.L.W.S., i.e. level (1). Thus, in Jennycliff Bay, critical level (2) is unrepresented.

At Wilderness Point an overlap occurs, due to the raising (by shelter) of the lower limits of *Littorina rudis*, *Chthamalus*, *Ascophyllum*, and *Fucus vesiculosus*, and to the absence of *Osilinus* and *Lichina*.

With regard to the lower limit of intertidal species, then, either two maxima or one may be recognized; but the M.L.W.N.-M.L.W.S. region is definitely critical for such species, unless a few are permitted to penetrate beyond M.L.W.S. under the influence of strong surf action.

Level (3) in Cardigan Bay marks the upper limit of sublittoral species such as *Laminaria digitata*, *Gibbula cineraria*, *Rhodymenia* and *Gigartina*. In the Plymouth neighbourhood the last two species may extend up beyond this level, but an additional species, *Himanthalia lorea* is introduced. This level is fairly constantly placed, at all localities, in the M.L.W.N. to M.L.W.N. – 1 ft. region.

Levels (4) and (5) in Cardigan Bay include the upper limits of distribution of the following species:

LEVEL (4): *Osilinus*, *Balanus balanoides*, *Littorina littorea*, *L. littoralis*, *Ascophyllum*, *Fucus vesiculosus*, *Gibbula umbilicalis*, *Nucella*, *Laurencia* and *Fucus serratus* (also of *Mytilus edulis*, which has not been studied, and of *Sabellaria alveolata*, which is infrequent, in the Plymouth neighbourhood).

LEVEL (5): *Patella vulgata*, *Lichina pygmaea*, *Pelvetia canaliculata*, *Chthamalus*, *Fucus spiralis*, and *Patella depressa*.

On Church Reef (1946), though *Chthamalus* and *Pelvetia* extend above E.H.W.S., *Patella vulgata*, *Lichina* and *Fucus spiralis* do not exist to as high a level as they do in Cardigan Bay; consequently this single critical level at Church Reef (1946) consists of level (4) plus part of level (5) of Cardigan Bay.

At Queener Point the two levels are distinct, and are equivalent to (4) and (5) of Cardigan Bay, with the following exceptions: *Osilinus*, instead of being included in (4), is now in (5); *Chthamalus* achieves its upper limit higher than (5); and *Littorina littorea*, *L. littoralis*, *Ascophyllum* and *Fucus serratus* are absent due to the violence of surf experienced at Queener Point.

The upper critical level at North Point does not include the upper limit of *Chthamalus*, which ends above it; of *Fucus vesiculosus*, *F. serratus* or *Laurencia*, which end below it; or of *Ascophyllum*, which is too infrequent to zone at this locality. Thus it represents parts of (4) and parts of (5).

The same is true of the single level in Jennycliff Bay. *Chthamalus* and *Pelvetia* end above it; *Laurencia* ends below it; while *Lichina* is unrepresented.

At Wilderness Point the two levels are equivalent to those of Cardigan Bay, with the following exceptions: *Osilinus* is absent; *Littorina littorea* is infrequent and was not included in the results, neither was *Laurencia*; *L. littoralis* (under the cover of *Pelvetia*) extends upshore to end in (5) and not in (4); the upper limit of *Littorina rudis* is lowered by the sheltered conditions, and comes to lie in (5) instead of well above it as it does in more exposed localities. However, the levels are more or less equivalent, and have been numbered accordingly.

Summarizing these results, it would appear that, while generalizations can be made with regard to certain levels on the shore being more critical than others for intertidal plants and animals, any arbitrary method of graphing specific limits and deriving critical levels from these graphs (as Colman, 1933, and the present worker have done) will inevitably yield somewhat inconsistent results at different localities. Both the number and type of species studied will be important; and any local modifications or variations in environmental factors are likely to have varying effects on the upper and lower limits of different species, and so to cause variation in the position of critical levels at different localities. The factor of exposure to wave action is obviously of great importance in this respect; there is often a considerable difference between the 'predicted' height of tides and their 'actual' or 'effective' height, which is determined by the amount of wave action and splash. Zoning species on a basis of predicted tidal levels will inevitably yield different results at different localities; and the difficulty is to evolve some method of assessing the actual, effective height of tides at localities exposed to varying degrees of surf action. Other modifying factors which may upset the scheme of vertical zonation and displace the critical levels are: rock slope, the presence of shading influences, the presence of thick algal cover, etc. Nevertheless, despite the discrepancies in the positions of critical levels at different places along the coast, certain generalizations can be made:

(*a*) The region between M.L.W.S. and M.L.W.N. is critical in the sense that the majority of intertidal plants and animals reach their lower limits here. Often two sets of such species may be distinguished: (1) those for which the neighbourhood of M.L.W.S. is critical, and (2) those which reach their lower limits in the M.L.W.N. region.

(*b*) While certain sublittoral species may succeed in penetrating into the littoral region, these generally extend only as high as a level just below M.L.W.N.

(*c*) Levels between E.H.W.N. and M.H.W.S. are critical for intertidal species in the sense that many of them reach their upper limits here; though some, normally limited in the M.H.W.N.-M.H.W.S. region, may be elevated by splash to above this.

(*d*) It is very clear, at all the localities without exception, that the region of the shore between E.L.W.N. and E.H.W.N. is the least critical for intertidal plants and animals. Here, not only are the relative times of submergence and emergence (together with the change in environmental conditions correlated with these states) regular, but the factor of 'non-tidal' exposure to the air is not introduced.

Colman (1933) and Chapman (1941) both discuss the significance of critical levels on the shore and the possible factors which may account for them. It would appear that far too little is known of the requirements of individual species (e.g. the relative periods of submergence and emergence which they require, or are able to withstand), and a study of these, correlated with the analysis of tidal data, is likely to prove the most promising approach to the problem.

SUMMARY

The work includes an investigation of the intertidal distribution of several species previously studied in Cardigan Bay. Twelve localities in the neighbourhood of Plymouth were selected for study, showing a range from conditions of extreme exposure to surf action to conditions of maximum shelter. The main features of rock configuration and surf action at the different localities are briefly described.

The method of investigation is described, and results obtained for the zonation of the fucoids on Church Reef are compared with the results of Colman (1933). It is concluded that the method of survey adopted in the present work yields results of a high degree of accuracy.

The horizontal and vertical distributions of the flora are described and related to the intensity of surf action. This is followed by a discussion of the effects of wave intensity and wave frequency on the distribution of algae in general. The importance of the frequency of wave shock in the mid-tidal region of the shore, and its influence on algal colonization, is stressed. An attempt is made to arrange the algae studied in order of decreasing tolerance of surf.

The distribution of the selected species of animals at the different localities is described; and a discussion follows on the effect of wave action as a presence or absence factor in horizontal distribution, and as a modifying factor on vertical zonation. The effect of surf on the size of individuals of certain species is also commented upon.

The relation of the plant and animal species to different percentage exposures to the air at different shore levels is discussed. Results obtained from an extensive survey of Church Reef, Wembury, are compared with those obtained from Colman's (1933) traverse survey of the same area, and with the Cardigan Bay results. The percentage air-exposure limits of species in the Plymouth neighbourhood are also compared with similar limits in Cardigan Bay. It is concluded that there is a great degree of similarity in intertidal zonation at the two localities, though certain species appear to be more tolerant of exposure to the air in South Devon than they are on the Cardiganshire coast.

The existence of 'critical levels' for intertidal species in Cardigan Bay and at five localities near Plymouth is investigated. It is shown that the position of such levels changes in relation to local variations in surf action, rock configuration, illumination, etc.; nevertheless the existence of critical levels is an actuality. Generally speaking, the following regions of the shore may be

described as more critical than others for littoral plants and animals: (*a*) from M.L.W.S. (or just below this) to M.L.W.N.; (*b*) just below M.L.W.N.; (*c*) from E.H.W.N. to M.H.W.S. The least critical levels on the shore are between E.L.W.N. and E.H.W.N.

The writer wishes to thank Prof. T. A. Stephenson for his help and criticism of the manuscript, and to acknowledge a grant from the Royal Society which made the work possible.

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NEW OBSERVATIONS ON THE DISTRIBUTION AND MORPHOLOGY OF THE AMPHIPOD, *GAMMARUS ZADDACHI* SEXTON, WITH NOTES ON RELATED SPECIES

By Sven G. Segerstråle

From the Zoological Museum of the University and the Laboratorium Hydrobiologicum
Soc. Scient. Fennicae, Helsinki-Helsingfors, Finland

(Text-figs. 1–7)

Editor's Note. This paper and that by Mr G. M. Spooner (this *Journal*, pp. 1–52), independently bringing forward certain new ideas on the taxonomy of *Gammarus zaddachi* and *G. locusta*, were received for publication simultaneously. As Mr Spooner's paper is a report of work largely carried out before the war, of which summarized results have already been referred to in print (e.g. Report of Council in this *Journal*, Vol. XXIV, pp. 444, 691; Huxley, *The Modern Synthesis*, p. 315), it is given precedence. The authors have since consulted each other over matters in which their contributions overlap, in particular over the taxonomic status of the new forms they distinguish and regarding the names to be applied to them. Dr Segerstråle has kindly consented to adopt the two new names introduced above by Mr Spooner, and to make considerable alterations to his original manuscript.

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INTRODUCTION

As is well known, the species *Gammarus zaddachi*, established by E. W. Sexton in 1912 on material from European brackish and fresh-water localities, has caused great confusion among zoologists, as the characteristics distinguishing it from various related species, particularly *Gammarus locusta*, *G. duebeni* and *G. pulex*, have been very frequently disregarded. This confusion still persists to-day—that is amply shown by the material received for the present investigations from various museums.

In view of the drawbacks brought about by this confusion, not the least on account of the fact that *G. zaddachi* has been accepted as a typical salinity indicator in ecological work while, on the other hand, *G. locusta* is a favourite object for physiological investigations on osmotic regulation in water animals, zoologists are deeply indebted to Mrs Sexton for a paper, published in this *Journal* in 1942, the aim of which was to clear up the problems that have arisen around *G. zaddachi*. In this paper the author discussed the whole literature on the subject, and was in many cases able to correct previous errors by re-examining the original material. In addition, the author gave a new detailed description of the two forms of the species, the 'saline' and the strikingly hairy 'fresh-water' one, accompanied by numerous excellent figures. Finally, the paper contained a comparison between *G. zaddachi* and the species with which it has most often been confused.

The main differences between *zaddachi* and *locusta* mentioned, and as a rule depicted in Sexton's paper, refer to the setose armature of the peduncle of antenna 1 (in *zaddachi*, numerous clusters of well-developed hairs present; in *locusta*, the peduncle almost glabrous); to the shape of gnathopod 2 (in *locusta*, narrower proportionately, etc.); to the shape of side-plate 4 (in *zaddachi*, inferior margin almost semicircular; in *locusta*, lower portion deep and almost rectangular); to the epimeral plates 2 and 3 (in *zaddachi*, hind-corners subacute; in *locusta*, acutely produced); to the pleon segments 4–6 (in *zaddachi*, dorsal humps only slightly raised; in *locusta*, elevated and prominent); etc.

A characteristic referring to the head sinus should be added to these principal points of difference. In *zaddachi* the sinus is much deeper than in *locusta*. Sexton says that both the species have a slight sinus, but in her figures (1 and 19) the divergence is clearly seen. The deep head sinus in *zaddachi* has been correctly depicted already by Stephensen (1940, fig. 40, I, II, p. 317), in connexion with the description of an atypical form of *locusta*, occurring in his material from northern Norway and adjacent waters; as seen below, it is in reality identical with *G. zaddachi*. To show the difference in shape of the epimeral plates of both species Fig. 1 may be given (cf. also Sexton's text-fig. 1). Fig. 2 illustrates the differences between *zaddachi* and *duebeni*, mentioned in Sexton's paper.

A historical remark may be added here. Oddly enough, it seems probable that the species nowadays regarded as the true *locusta* is not identical with the form found by Linnaeus in 1741 on the seashore at Gothland and named by him (in 1745) *Cancer macrourus coeruleus*, and later on (1761, etc.) *C. locusta*, but rather that he had had to do with *Gammarus zaddachi*. The famous naturalist points out in his description that the last pair of legs had the inner ramus shorter than the outer. As the difference in length is very small in the 'modern' *G. locusta*, but in *G. zaddachi* constitutes one of the most striking characteristics, and, furthermore, as *zaddachi* occurs very commonly together with *locusta* on the shores of Gothland (see below, pp. 236–9), it appears definitely more probable that the amphipod observed by Linnaeus belonged to *zaddachi*. A similar view has already been expressed by the Swedish zoologist Liljeborg. In his account of the Scandinavian species of the genus *Gammarus* (1855) he emphasized that the species meant by Linnaeus was obviously not *G. locusta* M. Edwards (in which the rami of the last uropods are, as in the *locusta* of the present day [depicted by Sars etc.], 'presque égaux entre eux' [M. Edwards, 1840, p. 45]). He therefore gives this species the name *mutatus* and regards the '*locusta*' found in the Baltic by Zaddach (1844, 1878), i.e. the same which in 1912 was called *G. zaddachi* by Sexton, as Linnaeus's species. In the diagnosis of the two species Liljeborg especially points out the differences in the relative length of the inner ramus of the last uropods, giving for *mutatus* 'rami pedum spuriorum ultimorum circiter aequales' and for *locusta* 'rami pedum spuriorum ultimorum insigniter inaequales, interior exteriore saltem tertia parte minor'.

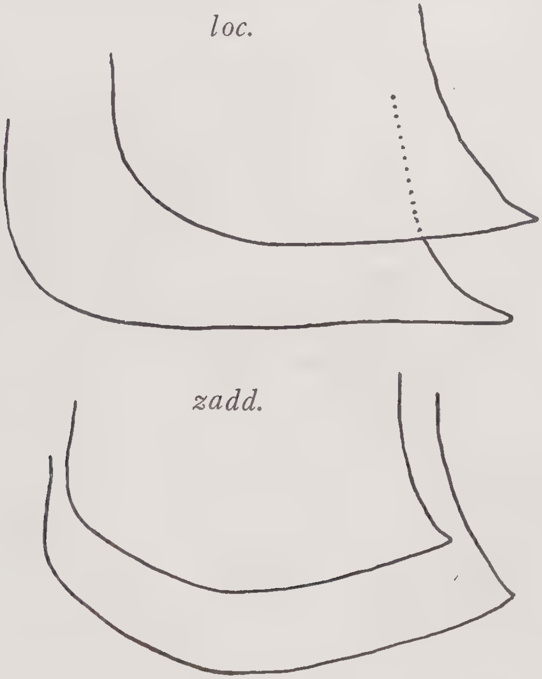

Fig. 1. Second epimeral plates of *Gammarus zaddachi* and *G. locusta* (two of each; males), to show the difference in shape of hind-corner. Setae and spines omitted. Material from the Baltic.

The fact that already Liljeborg separated the two forms of *Gammarus* mentioned above into distinct species, may, if only the priority of the nomenclature suggested by him is taken into consideration, motivate changing of the names *locusta* and *zaddachi*, used nowadays, into *mutatus* and *locusta* respectively. But in view of the great new confusion which no doubt would be the consequence of this change, the present author has the decided opinion that the modern names should be retained as '*nomina conservanda*'. This idea is supported by the fact that Liljeborg erroneously listed the independent species *G. duebeni* as synonymous to *G. locusta*, thus making the value of the diagnosis of this species somewhat doubtful.

In connexion with studies on the *Gammarus* fauna carried out in the Finnish coastal waters since 1941, the present author has obtained results which cast a new light on the distribution and ecological character of the saline form of *G. zaddachi* and which also complete our knowledge of the morphology of this and the fresh-water form of the species in essential points. These results which, I hope, may considerably facilitate the recognition of *G. zaddachi*, are dealt with in the present paper. In connexion with this subject the relationship between *G. zaddachi* and the closely allied species *G. setosus* and *G. wilkitzkii* will be discussed.

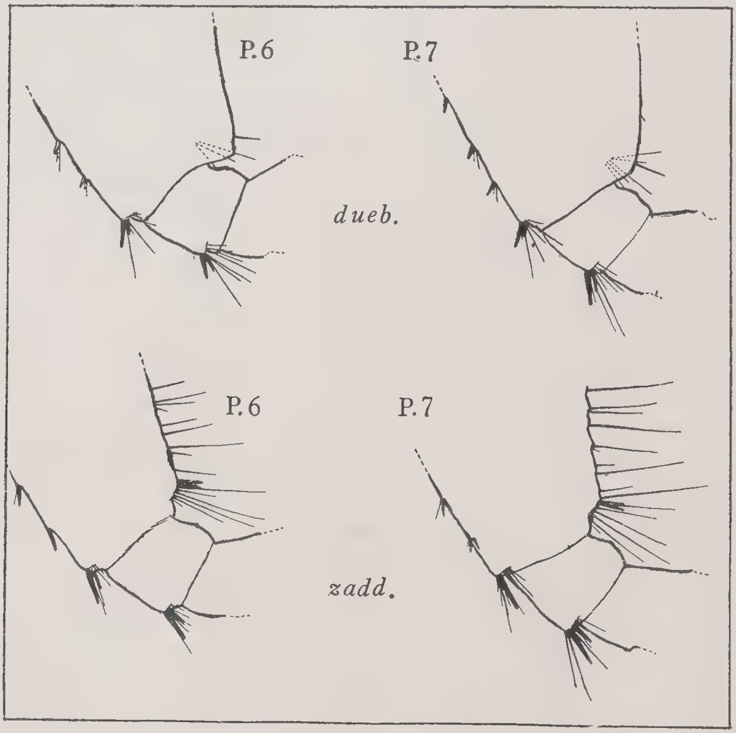

Fig. 2. Segments 2–4 of the peraeopods 6 and 7 of *Gammarus duebeni* and *G. zaddachi* fresh-water form (=ssp. *zaddachi*, according to Spooner; see p. 5), to show the difference between these species in the shape of the postero-distal angle of the basal segment. In the former species this is much more produced (especially in the 6th peraeopod) and lacks the strong spines present in the latter. (From Segerstråle, 1946.)

The author feels deeply indebted to Mrs E. W. Sexton (Marine Biological Laboratory, Plymouth) for her most valuable and kind help in sending material and discussing in letters questions concerning the subject. He is also indebted to the late Museumsinspektör K. Stephensen, of the Museum of Copenhagen, for his kindness in repeatedly supplying collections of *Gammarus* from Danish and Arctic waters. The other museums from which material was received for the present investigation, with the names of those to whom the author's thanks are similarly due, are as follows: Bergen Museum, Conservator H. Tambs-Lyche; British Museum, Dr Isabella Gordon; State Museum of Natural History, Stockholm, the late Prof. Dr Sixten Bock; Zoological Museum, Berlin, Prof. Dr Adolf Schellenberg. In addition, Mr D. M. Reid (Harrow) and Cand. phil. Erik Dahl (Lund) have kindly sent samples of various forms of *Gammarus*.

In total the material available embraces collections from the northern Atlantic and the Arctic (Massachusetts, Labrador, Greenland, Iceland, Norway, Spitsbergen, Murman Coast, Novaya Zemlya), the North Sea (Heligoland, coast of Denmark), the Cattegat, the waters around the Danish Isles, and the Baltic.

As mentioned already by Spooner, in his paper in this *Journal*, pp. 1–52 (see Editorial note, p. 219), the results obtained by him and by the present author partly overlap. Thus we have both distinguished Sexton's 'fresh-water form' from two other types of *zaddachi* and have described it. Thanks to the good offices of the Editor we have had the opportunity of going through our papers reciprocally before publication. The name *G. zaddachi* subspecies *zaddachi* given by Spooner to the above-mentioned form will be used also in the present paper. Another form found by both of us and designated subspecies *salinus* by Spooner will also be quoted here under his name. The third form which has been studied mainly by the present author will be described below as subspecies *oceanicus*.

The author wishes to present his thanks to Mr Spooner for most valuable comments and suggestions in letters.

SURVEY OF THE RESULTS CONCERNING THE DISTRIBUTION AND MORPHOLOGY OF *GAMMARUS ZADDACHI*

The distribution of the saline form.[1] The saline form of *G. zaddachi* (also formerly called the brackish-water form by Sexton) has hitherto been recorded only from waters with reduced salinity (the southern coast of the Baltic and the estuary of the Elbe, etc.), and has consequently been regarded as a typical brackish-water animal. In reality, this form is, however, mainly marine as, besides being distributed in brackish water, it is also widely found in the northern Atlantic and the Arctic (Fig. 4). In the samples from these waters, labelled *locusta*, the saline form is extremely common, whereas the true *locusta* is almost entirely lacking (besides *zaddachi* the Arctic samples of '*locusta*' frequently contain the species *G. setosus* and *G. wilkitzkii*). Structurally the form in question agrees strictly with the saline one living in the Baltic in all essential characteristics, the only difference being its size, which is much larger (body length up to 38 mm.).[1]

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[1] As shown by Spooner, Sexton's 'saline form' of *zaddachi* embraces the subspecies *salinus*, erected by him, as well as the subspecies *oceanicus*, described for the first time in this paper. The 'saline form', spoken of here, refers to the latter subspecies.

The northernmost localities from which records of the true *locusta* originate are situated on the north-east coast of Iceland (Bakkafjordur; Cop. Mus.) and northern Norway (Loppa, *c.* 70½° N.; Stephensen, 1940, p. 318). Thus, the species does not penetrate as far north as does the saline form of *zaddachi*. *Locusta* also does not nearly attain the same size as this form (maximum observed length of *locusta* 29 mm.; Stephensen, 1940, p. 318; a clear difference seen also in the Baltic). The previous literature records of Arctic specimens of *G. locusta* greater than *c.* 30 mm. might consequently refer to the saline form of *G. zaddachi* (or to the likewise very large allied species *G. setosus* and *G. wilkitzkii* which also hitherto have frequently been determined as *G. locusta*). The saline form of *G. zaddachi* is very euryhaline; in this respect it distinctly surpasses *G. locusta* (for details, see pp. 236–8).

The existence in the northern marine areas of a very *zaddachi*-like form of *G. locusta* has already been realized by Stephensen. In the above-mentioned important paper on the Amphipoda of northern Norway and Spitsbergen with adjacent waters (1940), he points out that the material of *G. locusta* (by him named *G. locusta locusta*) included, besides the typical form, also a deviating one which was much more common in the collections, and which in certain respects agreed with *G. zaddachi*, particularly in the shape of the 4th side-plate. As the collections used for the present investigation contain a number of samples from Stephensen's material, the author has had the opportunity of examining them. The form discussed by Stephensen is a typical *G. zaddachi*, saline form. Stephensen's including it in the species of *locusta* is partly accounted for by the incorrect records of the head sinus in *G. zaddachi* given in previous literature.

The morphology of the saline and the fresh-water form. As is well known, the setose armature of the two forms differs greatly, as it is much more developed in the fresh-water form, especially on the hinder peraeopods, the pleon segments 4–6, the telson, and the uropod 3. It is, however, striking that the difference in hairiness between the 1st antennae of both forms, although generally quite distinct, has not been observed so far.[1] This may probably be explained by the aim of the descriptions of *zaddachi* mainly having been to point out the characteristics which separate the species from *locusta*; with respect to the 1st antenna, namely, both forms of *zaddachi* clearly differ from this species. But, on the other hand, the comparatively poor hairiness of the antennae in typical saline specimens of *zaddachi* obviously gives it a resemblance to *locusta* great enough to cause confusion with this species. The difficulty of identification has been augmented by the shortness of the peduncle of the 1st antenna in the saline form, a characteristic which has also been overlooked.

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[1] The author's determination of the Baltic saline form has kindly been confirmed by Mrs Sexton.

The above-mentioned inequality in length of the peduncle of the 1st antenna shows that the view prevailing nowadays of the differences between the saline and the fresh-water form being confined to the strong hairiness of the latter is not correct as the structure of the two forms also differs. In addition, the present investigation has revealed a second structural disparity, viz. in the relative length of the 2nd antenna in the fresh-water form being, in spite of the longer peduncle of the 1st antenna, distinctly greater than in the saline one.

Furthermore, the study of freshly captured animals from Finnish waters has shown that the body colour differs in the two forms of *zaddachi*. The difference is mainly caused by the existence in the fresh-water form of a pattern of transverse and longitudinal bands on the dorsal part of the body; in the saline form there is no pattern. Mrs Sexton's not having observed the divergence is due to the fact that her material consisted only of preserved animals; in alcohol and formol the pattern is completely deleted.[2]

Finally, the fresh-water form is smaller in size, even in comparison with the Baltic saline form which lives together with the former; if the large Arctic saline form is subjected to the comparison the difference is of course much more marked.

It may be added that the investigation of the comparatively extensive material available to the present author, containing among others the large Arctic specimens, has considerably widened the variation range for certain characteristics (number of spines on pleon segment 4–6, number of spines and setae on the telson, number of joints on the flagella of the antennae).

The 'combined' form. Transitional forms between the saline and the fresh-water forms of *G. zaddachi* have previously been found by several authors, mainly in the Baltic (Sexton, 1912, 1913; Schellenberg, 1934; Höfken, 1937; Dahl, 1944).[1] Specimens of this type are common also in the material from brackish areas available to the present author. Höfken emphasizes that these forms are not properly transitional, but combine characteristics of the saline and the fresh-water form (called by him *G. locusta* and *G. zaddachi*). This agrees with Dahl's statement that the specimens in his material from the Baltic, more or less intermediate between both forms (by him determined *G. locusta* f. *locusta* and f. *zaddachi*), have rather setose antennae (= fresh-water characteristic) but otherwise are very sparsely provided with hairs (= saline characteristic). In the collections from the Baltic examined by the present author this peculiar combined type is abundant. It has proved to be identical with Spooner's subspecies *salinus*.

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[1] Sexton (1942, p. 597) states: 'In all the animals, saline as well as freshwater, both peduncles and the flagella carry on the under margin dense tufts or clusters of long stiff outstanding setae, some of each cluster extending far beyond the rest.' Strictly, however, the records given (on pp. 597 and 600) of the number of hair clusters on the peduncle of antenna 1, as well as of the length of the peduncle, hold good only for the fresh-water form.

I can now add that Spooner, too, has noted differences in setation of the antennae between the fresh-water and those 'saline' animals which are here called *oceanicus*.

[2] As Sexton mentions (1942, p. 593) that 'the chitinous cuticle varies in the two forms, being thick, strong and opaque in the freshwater, thin and transparent in the brackish water specimens', this difference, according to records kindly given by Mrs Sexton to the present author in a letter, is obviously not real, but due to different preserving methods.

In the following account details will be given of the morphology and distribution of the different forms of *zaddachi*, as observed in the material studied (distribution records from other areas included).

As will be shown, the combination of the following characteristics is diagnostic of the new subspecies *G. zaddachi oceanicus*: (1) the shortness and sparse setation of the peduncle of antenna 1; (2) the sparse setation of the hinder peraeopods, the pleon segments 4–6, and the telson. (In the description a characteristic from the last peraeopod and the telson has been chosen as indicator of the hairiness of the hinder parts of the body. With respect to this character, *oceanicus* shows almost complete agreement with *salinus*.)

Unless otherwise stated, the descriptions refer to the *male* (the female has been less thoroughly studied; most characteristics are somewhat less marked in this sex). The records given refer to specimens of at least *c.* 8 mm. in length (in smaller animals the characteristics are mostly not fully developed). All measurements are taken from the tip of the rostrum to the insertion of the telson.

In the list of synonyms an asterisk designates that the author has had the opportunity of examining specimens used for the paper concerned.

Gammarus zaddachi Sexton subsp. **oceanicus** subsp.nov.

SYNONYMS

Sexton, 1912, 1913, 1942; *G. zaddachi*; brackish-water or saline form *in part.*, cf. footnote, p. 223.

*Stephensen, 1917: *G. locusta* var. *Zaddachi*, *in part.*; intermediate form between *G. locusta* and *G. locusta* var. *Zaddachi* (*in part.*). 1940: *G. locusta locusta*, *in part.*

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[1] Also the form, found by Poulsen in Danish waters and determined *G. zaddachi* (Poulsen, 1932, p. 6 and fig. 3), seems to belong to the intermediate type. According to Spooner (p. 35), in reality the animals regarded as intermediates by Sexton generally belong to the fresh-water form (= subsp. *zaddachi* Spooner).

*Hellén, 1919: *G. locusta, in part.*
*Blegvad, 1922: *G. locusta, in part.*
*Segerstråle, 1933: *G. locusta* (*in part.*). 1944: *G. locusta* f. *typica.*
*Schellenberg, material sent to the author: *G. locusta.*
*Valovirta, 1935: *G. locusta* f. *typica.*
Höfken, 1937: *G. locusta.*
*Suomalainen, 1939: *G. locusta* (*in part.*).
*Dahl, 1944: *G. locusta* f. *locusta.*

MORPHOLOGY

Maximum size. Male: Arctic 38 mm. (Stephensen, 1940, pp. 318, 320; north Norway), Baltic 26 mm. (Schellenberg, 1934, p. 11, records a '*G. locusta*', captured near Kiel and measuring 32 mm.; probably a male of *G. zaddachi oceanicus*). Female: Arctic 28 mm. (Stephensen, 1940, p. 319; north Norway), Baltic 22 mm.

Body colour (studied in freshly captured specimens from Finnish waters). Greyish, yellowish, or greenish brown, semi-transparent; usually darker in the female. No dorsal pattern nor, usually, red spots of oil globules on the sides of pleon segments 1–3.

Setose armature of peraeopods, pleon segments 4–6, *telson, and uropods.* Weak development of the setae, as seen in Sexton's figures (1942, saline form). Peraeopod 7, longest seta in subapical cluster on hind margin of segments 4 and 5 not surpassing tip of spines in the same cluster (Fig. 3 *g* in the present paper).[1] Telson, longest apical seta shorter than distance from its insertion to tip of subbasal spines (Fig. 3 *e*, *f*).[2] In marine specimens the telson setae may be comparatively long and partly feathery (Fig. 3 *f*).

Length of antenna 2 *in percentages of antenna* 1, from 18 males, length 13–20 mm., from the Baltic, Iceland and Labrador; specimens with broken or regenerating flagella excluded: 68–77, average 73%.

Maximum number of segments in the flagella (body length in brackets):

		Male	Female
Antenna 1:	primary flagellum	57 (31 mm.)	38 (25 mm.)
	accessory flagellum	10 (31 mm.)	11 (25 mm.)
Antenna 2		21 (33 mm.)	22 (25 mm.)

Length of peduncle segments of antenna 1 (Fig. 3 *a–d*; segment 1 measured from tip of the rostrum to distal end of the segment). Ratio of length of segments 2 and 3 combined to that of segment 1, from 1·0:1 to 1·3:1, generally *c.* 1·1:1. Length of segment 3, 0·4–0·5 of that of segment 2. The end of the

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[1] The difference in hair development between *z. zaddachi*, on the one hand, and *z. oceanicus* and *z. salinus*, on the other, is more marked on the posterior than on the anterior margin of the hinder peraeopods.

[2] This method for measuring the seta concerned has been chosen instead of comparison with the corresponding spines in order to reduce the inaccuracy of results arising from the variability of the spine length.

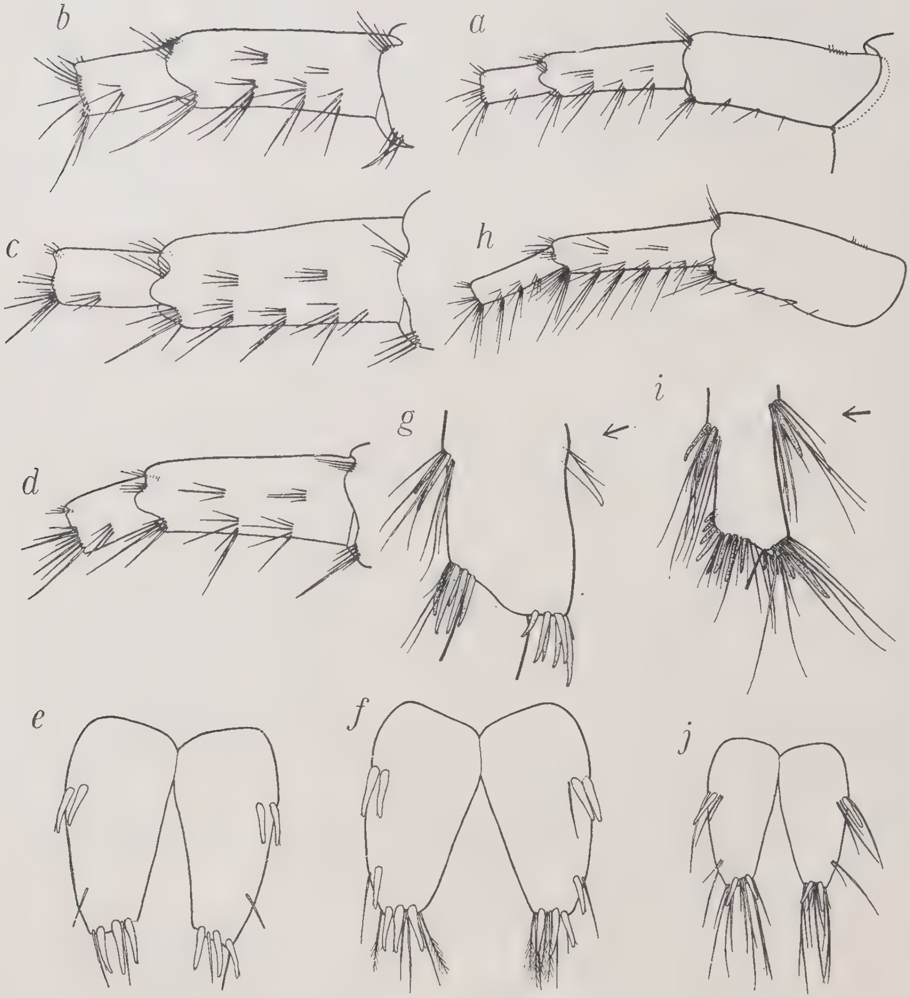

Fig. 3. *Gammarus zaddachi* (male). *a–g*, *z. oceanicus*; *h–j*, *z. zaddachi*. *a–d*, peduncle of 1st antenna (right, from the inner side; in *b–d* only segments 2 and 3 depicted): *a*, south-west Finland (body length 16 mm.); *b*, north Norway (27 mm.); *c*, north Greenland (31 mm.); *d*, north Norway (27 mm.). *e–f*, telson: *e*, north Norway (26 mm.); *f*, Massachusetts (26 mm.). *g*, peraeopod 7, distal part of segment 5 and proximal part of segment 6, west Greenland (27 mm.; the arrow shows the cluster used as a characteristic in the diagnosis; the specimen depicted has comparatively long setae on the anterior margin of segment). *h*, peduncle of 1st antenna, south Finland (16 mm.). *i*, peraeopod 7 (for part depicted and arrow, see above), south Finland (19 mm.; the specimen has unusually short setae; for maximum length, see Sexton 1942, fig. 12). *j*, telson, south Finland (18 mm.).

peduncle (when stretched forward, to continue the dorsal line) reaches at least as far as to the end of segment 4 of antenna 2 and at most to somewhat less than half the length of segment 5, generally to about a quarter of this joint.

Number of hair clusters on the under-margin of peduncle segments 2 *and* 3 *of antenna* 1 (*including apical cluster*) (Fig. 3). Segment 2, 3–5, generally 4, clusters; segment 3, 1–2.

Pleon segments 4–6, *spine formula:*

4th segment	3–6 : 2 : 3–6
5th segment	3–5 : 2 : 3–5
6th segment	2–3 : 2 : 2–3

Telson, number of spines and setae:

	Spines	Setae
Apical	3–4	1–5
Subapical	0–1	0–2
Subbasal	1–3	0–2

Uropod 3 *inner ramus*, length about three-quarters that of the outer, excepting in large marine specimens in which it may be up to seven-eighths.[1]

ADDITIONAL NOTE

The following differences between *z. zaddachi* and *salinus* observed by Spooner, have proved to exist also between the former subspecies and *oceanicus* (material from Finnish waters).

As does *salinus*, *oceanicus* differs from *z. zaddachi* in the following respects: (1) accessory flagellum, number of segments and length somewhat greater; (2) gnathopod 2, a little narrower and hinder margin clearly bulging (in *z. zaddachi* almost straight); (3) epimeral plate 3, posterior distal angle distinctly more acutely produced (epimeral plate 2, difference less pronounced); (4) distal segments of last peraeopod, somewhat more slender; (5) last uropod, inner ramus a little longer. The measurements—certainly few in number—of characteristics 1, 4 and 5 fall within or very near the variation limits given by Spooner for *z. zaddachi* and *salinus*.[2]

DISTRIBUTION

The form in question is widely spread in the northern Atlantic (material from waters south of the North Sea not available) and in the Arctic, but occurs abundantly also in the brackish water of the Baltic (observed minimum salinity in places of capture *c.* 2·5 °/₀₀) (see map of the Baltic in Fig. 6; for details see p. 236).[3] Depth records: 0–25 m.

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[1] It is a common feature in the amphipods that the inner ramus of the last uropods increases with age, as is well known.

[2] The author has not found calceoli in the (mature) female of *z. zaddachi*. These organs were lacking also in the examined females of *oceanicus* (Spooner mentions that he often found calceoli in the female of *z. salinus* but not of *z. zaddachi*).

[3] Spooner has now shown (p. 43) that the subspecies in question occurs also in northern Scotland.

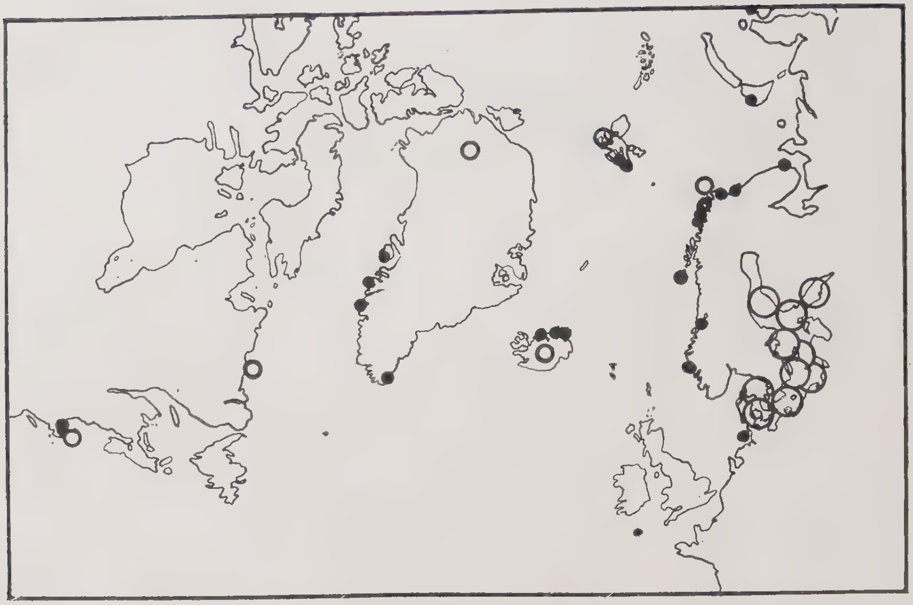

Fig. 4. The distribution of *Gammarus zaddachi oceanicus* according to the material investigated (samples not available from waters south of the southernmost localities seen in the map). Large open rings: more thoroughly studied areas (for details, see p. 236). Small open rings: record of locality not exact or insufficient ('Massachusetts', 'Labrador', 'North Greenland, Norsovak', 'Iceland', 'Spitsbergen, Kobbe Bay', 'Finmarken').

Gammarus zaddachi Sexton subsp. **zaddachi** Spooner 1947.

SYNONYMS

Hoek, 1889: *G. locusta*, var. A.[1]
Sexton, 1912, 1913, 1942: *G. zaddachi*, fresh-water form.
Tesch, 1915: *G. locusta*, var.[1]
*Stephensen, 1917: *G. locusta* var. *Zaddachi* (*in part.*); intermediate form between this form and *G. locusta* (*in part.*). 1927: *G. duebeni* (at least *in part.*).
*Hellén, 1919: *G. locusta* (*in part.*); *G. duebeni* (*in part.*).
Tesch, 1922: *G. locusta*, Hoek's var. A.

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[1] This form, which already Sexton (1942, p. 582) has regarded as belonging obviously to *zaddachi*, seems to be identical with *z. zaddachi*, owing to the presence of long setae on pleon segments 4–6 and telson (Hoek's figs. 11′ and 11″, pl. X) and of red spots on the pleon; the extremely low salinity in some of the recorded localities is also a favourable indication.

The two specimens, described by Tesch (1915) from the southern part of the North Sea and regarded by him as closely related to Hoek's var. A, might also belong to *z. zaddachi*. Their occurrence in the open sea was due presumably to transport from adjacent coastal waters with reduced salinity.

Gurjanova, 1930: *G. zaddachi*.[1]
Dementieva, 1931: *G. setosus* f. *baltica*.[2]
Schijfsma, 1931: *G. locusta*, Hoek's var. A.
*Poulsen, 1932: *G. duebeni*. 1933–36: *G. duebeni* (*in part*.).
Oldevig, 1933: *G. locusta* (*in part*.).
*Segerstråle, 1933: *G. locusta* (*in part*.). 1944: *G. zaddachi*.
*Schellenberg: *G. locusta* f. *zaddachi* (determination of samples, Helsinki Mus.).
Serventy, 1935: *G. zaddachi*.[1]
*Valovirta, 1935: *G. locusta* f. *zaddachi*.
Lucks, 1937: *G. locusta-zaddachi*.
Höfken, 1937: *G. zaddachi*.
*Reid, 1939: *G. sarsi*. 1945: *G. ochlos* nom.nov. (=*G. sarsi*).[3]
*Suomalainen, 1939: *G. locusta* (*in part*.).
*Dahl, 1944: *G. locusta* f. *zaddachi*, *G. locusta* f. *setosus*.

MORPHOLOGY

Maximum size. Male 22 mm., female 15 mm.

Body colour (studied in freshly captured Finnish specimens). Ground colour distinctly lighter than in *oceanicus*: pale greyish green, sometimes greyish yellow. On the dorsal parts of the body a darker pattern, pale or darker brownish green in colour (Fig. 5). This pattern, the colour intensity and extension of which varies considerably, is composed of a system of transverse and longitudinal bands.[4] *Transverse bands*. Present on the posterior margin of head and of all body segments, excepting pleon segments 4–6 (the colour effect of these bands is augmented by the partial intervention of each segment into the preceding one; on that account these portions seem especially dark). On account of the bands the body of the animal is distinctly transversely striped. On the anterior margin of head, the first peraeon segment, and all pleon segments, transverse bands also occur. Finally, there are median bands on the peraeon segments (excepting the 1st) and on pleon segments 1–3 (the pleon bands are comparatively strongly developed). The median bands

[1] In view of the very low salinity in the locality, where Gurjanova captured '*zaddachi*' ('almost fresh' water, in the estuary of the Sewernaja Dvina), she very likely had to do with *z. zaddachi*. The same conclusion holds good for the specimens caught by Serventy at the more inland stations in the estuary investigated (River Deben, England).

[2] The comparatively slight head sinus depicted by Dementieva (fig. 10) is conceivably due to somewhat inaccurate drawing or may refer to a specimen of the true *locusta*; the telson figured is of typical *z. zaddachi* shape.

[3] The author has found no essential differences between this very small form (length *c*. 6 mm.), described on material from the brackish Loch of Stennes, Orkney, and mature specimens of *G. z. zaddachi* of the same size from the Baltic (material kindly sent by Mr Reid).

[4] Palmer (1933, p. 65) observed brown transverse bands on the body segments and on the appendages of a form of *G. zaddachi*, captured in brackish water on the English coast; it was probably *z. zaddachi* or *z. salinus*.

are frequently more or less reduced, sometimes missing, even on the pleon. *Longitudinal bands.* A median band, more strongly developed on the pleon but sometimes even here strongly reduced (see Fig. 5), runs along the whole length of the body. As a rule it is accompanied on both sides by a band, more developed on the peraeon. The colour pattern is observed also on the antennae (peduncle, flagella), on the peraeopods (especially on segments 1,

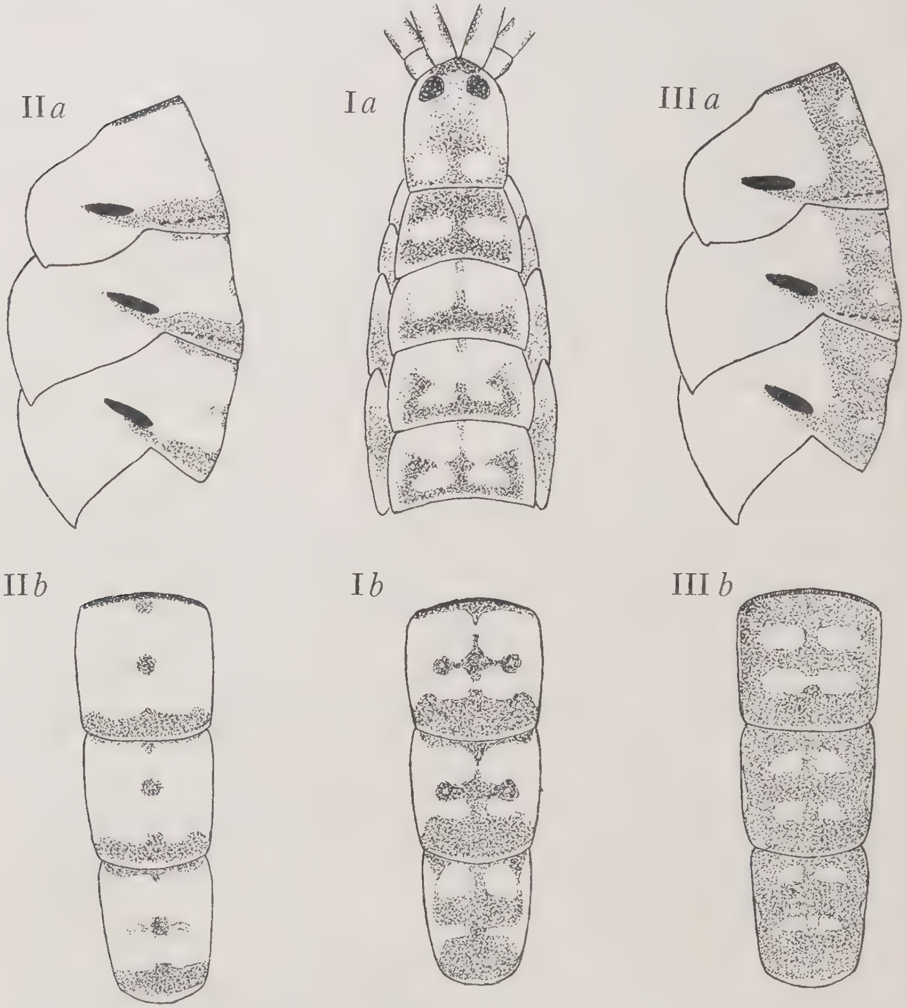

Fig. 5. The pattern in *Gammarus z. zaddachi*. (Material from the south coast of Finland; males.) Three specimens (partly) depicted, to show variation. I *a*, anterior part of body; I *b*, pleon segments 1–3 of the same animal. II *a* and III *a*, pleon segments 1–3 of two other animals, from the side; II *b* and III *b*, the same segments from above. The black oblong patches show the position of the red spots of oil globules.

3, 5–6), uropods and telson, and, weakly, on the side-plates. A pattern resembling the one just mentioned has been described by Sexton (1939) in *G. tigrinus*.

On the sides of pleon segments 1–3 there are almost invariably red spots of 'red oil globules', known from various other species of the genus *Gammarus* and mentioned in *G. zaddachi* by Sexton (cf. also Palmer, 1933). These are shown in Fig. 5. The pattern and the red spots disappear in preserved animals.

Setose armature of peraeopods, pleon segments 4–6, *telson and uropods.* Strong development of the setae, as seen in Sexton's figures (1942, fresh-water form). Last peraeopod, longest seta in subapical cluster on hind margin of segment 5 surpassing end of the segment (Fig. 3 *i* in the present paper). Telson, longest apical seta longer than distance from its insertion to insertion of subbasal spines (Fig. 3 *j*). Number of telson setae, see below.

Length of antenna 2 *in percentages of antenna* 1, from 17 males from the Baltic and the Danish lake Lammefjordssöen, length 13–20 mm.: 78–89, average 84%.

Maximum number of segments in the flagella (body length in brackets):

		Male	Female
Antenna 1:	primary flagellum	39 (21 mm.)	31 (15 mm.)
	accessory flagellum	8 (20 mm.)	6 (15 mm.)
Antenna 2		19 (20 mm.)	14 (15 mm.)

Length of peduncle segments of antenna 1 (Fig. 3 *h*; for measuring method see p. 227). Ratio of length of segments 2 and 3 combined to that of segment 1, from 1·3:1 to 1·7:1, generally *c.* 1·5:1. Length of segment 3, 0·5–0·7 of that of segment 2. End of peduncle reaching at least to about one-fifth, as a rule to somewhat less than half the length of segment 5 of antenna 2.

Number of hair clusters (including apical cluster) on the under-margin of peduncle segments 2 *and* 3 *in antenna* 1 (Fig. 3). Segment 2, 5–9 clusters, generally 6–7; segment 3, 3–5, generally 4.

Pleon segments 4–6, *spine formula:*

4th segment	2–3 : 2 : 2–3
5th segment	2–3 : 2 : 2–3
6th segment	2–3 : 2 : 2–3

Telson, number of spines and setae:

	Spines	Setae
Apical	1–3	4–17
Subapical	0–1	1–2
Subbasal	1	2–4

Uropod 3 *inner ramus*, length about three-quarters that of the outer.

DISTRIBUTION[1]

Brackish and, locally, fresh water in north and west Europe (highest salinity recorded *c.* 14–18 °/₀₀).[2] In the Baltic district found practically only in brackish water (the only exception being the record from the Danish Lake Lammefjordssöen, see below).[3]

Great Britain: see the numerous records given by Spooner. To them may be added Loch of Stennes, Orkney (brackish water, locality for *Gammarus ochlos* (*sarsi*) = *G. z. zaddachi*; see p. 231).
Ireland: Lakes Lough Nadarragh, Lough Keenaghan, Lough Awaddy, Lough Tullynabour, Lough Erne (Sexton, 1912).
France: Nantes and Belle-Île-en-Loire (Sexton, 1942, p. 583).
Belgium: see Spooner.
Netherlands: mouth of the Rhine and the Waal, Zuiderzee (Hoek, 1889; Tesch, 1922; and Schijfsma, 1931: *G. locusta* var. A).
Germany: see Spooner.
Denmark: Lake Lammefjordssöen (north-west Sealand; Copenh. Mus.); for marine localities see below. Spooner also gives several records from Danish waters.
Norway: Bolstadfjorden (near to Bergen; Bergen Mus.).
Baltic: all over the area, throughout the Gulf of Bothnia and the Gulf of Finland, to the Danish waters (for details see pp. 236–8).
? White Sea, mouth of the Sewernaja Dvina (see p. 231, footnote 1).

Gammarus zaddachi Sexton subsp. **salinus** Spooner 1947

As mentioned previously, in the *Gammarus* material studied by the author from the Baltic, a form of *zaddachi* was often found to which a peculiar combination of characteristics of the forms now named *z. zaddachi* and *z. oceanicus* is typical. The peduncle of antenna 1 is about as setose and elongate as in the former subspecies, whereas the hinder peraeopods, the pleon segments 4–6, and the telson are almost glabrous, as in the latter.

The opportunity given to the author of reading Spooner's manuscript and our reciprocal examination of British and Finnish material respectively has made it clear that the 'combined' Baltic form is identical with Spooner's subspecies *salinus*.

As this 'combined' type was captured only in waters where also *z. zaddachi* and *oceanicus* occurred, it seemed possible to the author at the first sight that it represented a curious result of crossbreeding between these two forms. Now, however, Spooner's interesting statement of *salinus* and *z. zaddachi* being incapable of producing fertile eggs with one another has given evidence of the genetical independence of the former type, and thus has motivated the establishing of it as an independent subspecies.

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[1] In order to make the list more useful it has been completed by references to Spooner.

[2] Tesch, 1922, Zuiderzee (Hoek's var. A).

[3] Compare *Gammarus duebeni*, which, in this area, is confined to brackish water, though in western Europe, etc. it is found also in fresh-water localities (cf. Segerstråle, 1946).

As already indicated the separation of *salinus* from *zaddachi* is easy, whereas the limit between the former subspecies and *oceanicus* may sometimes appear to be vague, owing to the partial overlapping of the main distinguishing characteristics, viz. the length and setation of the peduncle of antenna 1. As to the latter characteristic which is more useful in practice, it is typical that *salinus* has at least six tufts on the under-margin of peduncle segment 2, against four tufts in typical *oceanicus*. But the range of variation of both subspecies also includes the tuft number of five, and this number seems to be comparatively common in *salinus*. As pointed out previously, the number of tufts on the last peduncle segment might, in such instances, be a reliable distinctive characteristic. In *oceanicus*, from purely marine localities, where the brackish *salinus* is not to be expected, more than two tufts have practically never been found by the author, whereas *salinus* ♂ typically has at least three.[1] Specimens with five tufts on the second peduncle segment and three on the third might consequently belong to *salinus*, not to *oceanicus*. In freshly captured animals also the colour will, presumably, prove to be a good distinctive characteristic. The examination of a number of such specimens of typical *salinus* from Finnish waters showed that they all had the pattern which is found in *z. zaddachi* (p. 231), though it was generally much less distinct than in that form (the red spots were also present in many specimens). Further observations on more extensive material are necessary, but the foregoing statements seem at any rate to make it very likely that the colour will prove an additional characteristic which reliably distinguishes *salinus* from *oceanicus*.

In the material from the Baltic specimens have also been observed in which the setation of the last peraeopods, or of the telson (the two characteristics chosen as indicator of the hairiness of the hinder parts of the animal), or of both, is somewhat more strongly developed than in typical *oceanicus*. The setose armature of antenna 1 in these specimens is never as sparse as in typical *oceanicus*. The author is inclined to suppose that these varieties belong to *salinus*.

Details of the distribution of *salinus* in the Baltic, as well as in Danish waters, are given in the following section. Regarding the occurrence of the subspecies outside this district, see Spooner (pp. 41–3).

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[1] The only exception refers to a couple of specimens observed in the material from Heligoland. They bear three hair clusters on the segment in question, and the length of the last peduncle segment compared with the length of the second segment is 0·6, against at most two and 0·5 respectively in the typical marine form. It does not seem quite impossible that these specimens have been transported to Heligoland from adjacent brackish waters on the continental coast (cf. the assumed transport in another case, p. 230, note 1).

The Distribution of *Gammarus zaddachi* and *G. locusta* in certain Waters

The Baltic and Denmark (excluding Randers Fjord and Ringköbing Fjord)

Material. Number of samples investigated (abbreviations of Museum names: Cop. = Copenhagen, Hels. = Helsinki-Helsingfors, St. = Stockholm): Finnish waters, *c.* 230 (Hels., and the author's collections); the archipelago from Stockholm to Kalmar, 12 (St.); coast of Blekinge, 4 (St.); Gothland, 20 (St.); Bornholm, 5 (St., Cop.); Danzig, 1 (St.); east of Rügen, 2 (Cop.); Rügen-Danish Isles, 12 (Cop.); The Sound, 3 (Cop., St.); Falster-Sealand, 6 (Cop.); Great Belt, 6 (Cop.); Little Belt and adjacent southern waters, 3 (Cop.); Ise Fjord, 2 (Cop.); Cattegat, 10 (Cop.); west coast of Denmark, 5 (Cop.).

Regarding the literature records, the surveys by Stephensen (1928, 1929), Oldevig (1933) and Schellenberg (1942) could not be used, as the differences between *G. locusta* and *zaddachi* are here not recognized. But the data published by Poulsen (1932) and Dahl (1944), though not correct in the species determinations, can be reinterpreted in the light of the samples of these authors' material available to the writer. From the south coast of the Baltic *G. zaddachi oceanicus* has been recorded (as saline form) by Sexton (1912, 1913) who also records, and figures, *locusta* from these waters.

Gammarus zaddachi oceanicus. This form is the main *Gammarus* in the Baltic and around the Danish Isles. It is lacking only in the 'innermost' parts of the Gulf of Bothnia and of the Gulf of Finland (Fig. 6; in the Gulf of Bothnia, which has been studied less thoroughly, the northernmost record of *oceanicus* is *c.* 63° 30′ N.) and other strongly diluted localities. In the Gulf of Finland the 'innermost' records (Virolahti: Kiuskeri and Pien Kalastaja) lie at the isohaline of *c.* 2·5 °/₀₀ salinity (surface, year average). On the south coast of Finland, from which area a great quantity of material has been investigated, the form in question greatly outnumbers *z. zaddachi* in the outer parts of the archipelago, at least as far eastward as in Pellinge, and even in a sample from the island Peninsaari (near Lavansaari, at 28° 2′ E.) *oceanicus* is clearly predominating (115 *oceanicus* against 4 *z. zaddachi*). On the Finnish coast *oceanicus* is especially common in the *Fucus* vegetation (cf. Segerstråle, 1944; *oceanicus* here called *G. locusta* f. *typica*). The bulk of the material of *oceanicus* originates from a depth of a few metres, but there are also a number of samples from the open sea between Rügen and the Danish Isles with depths of *c.* 20 m.

In the samples from the Cattegat *oceanicus* is sparsely represented and entirely lacking in the material from the Danish west coast.

Gammarus zaddachi zaddachi is represented in the material from the very end of the Gulf of Bothnia and the Gulf of Finland to the Sound (Isle Hven). In the 'innermost' parts of the Gulfs (Fig. 6) and other strongly diluted areas it is the only abundant *Gammarus* (in addition *G. duebeni* occurs here locally; cf. Segerstråle, 1946). The author found the amphipod in great numbers inhabiting the vegetation of *Phragmites* in estuarine localities. The animal is

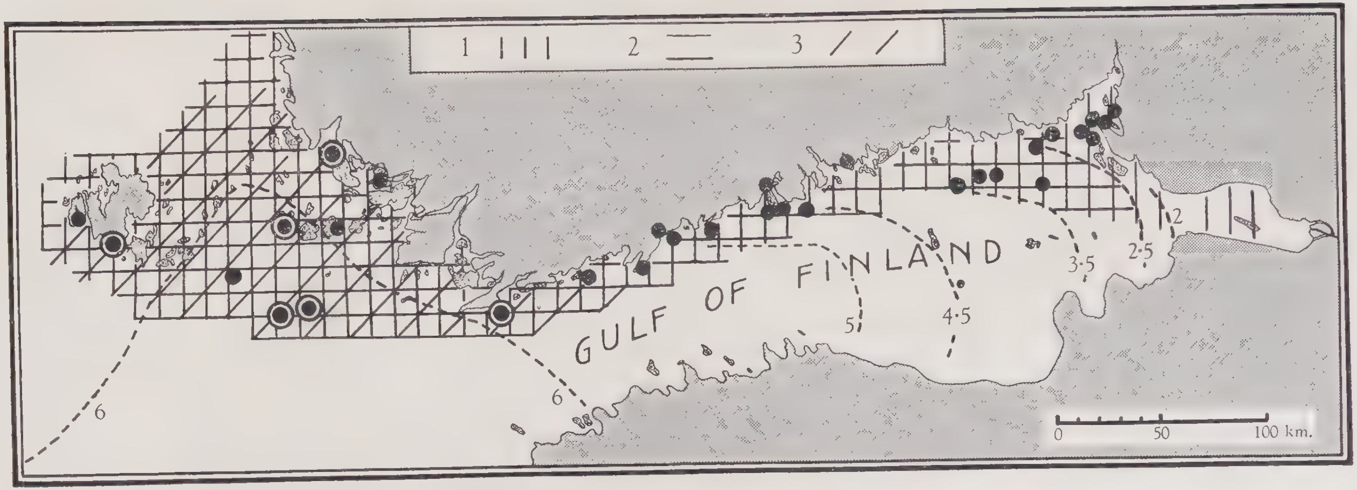

Fig. 6. The occurrence of *Gammarus zaddachi zaddachi* (1), *G. zaddachi oceanicus* (2), and *G. locusta* (3) along the north coast of the Gulf of Finland and in the south-west Finnish waters. The black dots show the origin of the material investigated. Localities for *G. locusta* indicated by rings. As seen, there are three *Gammarus* zones: (*a*) in the innermost part of the Gulf only *G. z. zaddachi* occurs, (*b*) westward from here to near the mouth of the Gulf *oceanicus* also is found, (*c*) the south-west waters are inhabited, in addition, by *G. locusta*. In addition, *G. z. salinus* occurs in the area, having about the same distribution as does *oceanicus*. Broken lines represent isohalines (°/₀₀).

common also in the Finnish archipelago, but, as mentioned above, less numerous than *oceanicus* in the *Fucus* vegetation of the outer zone. However, it generally occurs considerably more frequently than does *oceanicus* in very shallow water (with a maximum depth of half a metre or so) in this zone. From the Swedish waters represented in the material, i.e. the coast from Stockholm to Blekinge, and the coast of Gothland, there are numerous finds; also Dahl frequently captured *z. zaddachi* (for synonymy, see p. 231) in the latter waters. From deeper Baltic waters there is only one sample containing *z. zaddachi* taken east of Rügen, in 21 m. depth. The Danish material includes some samples containing *z. zaddachi*; they all refer to a depth of at most a few metres (Ore Strand: Sliphavnskrogen, Isefjord: Hovvig). But from this district there are also records given by Poulsen (1932), who captured the form in the waters between Sealand, Möen and Falster (for synonymy, see p. 231).

Gammarus zaddachi salinus. The subspecies shows, on the whole, the same limits of distribution in the area as *oceanicus*, but it is not present in the material from localities outside the Danish Isles. The type in question is found in most *Gammarus* samples, generally in small numbers, but locally it occurs in striking abundance. This phenomenon is observed in localities of quite different natures, viz. on the one hand in parts of the Finnish archipelago, which are not exposed to the open sea, and on the other in the open waters between Rügen and the Danish Isles and on the coast of the Great Belt (at Nyborg).

Gammarus locusta. Most of the previous records of this species from the Baltic area actually refer to *G. zaddachi*, mainly to subsp. *oceanicus* (for synonymy, see p. 227).[1] But *G. locusta* is also widely distributed in the Baltic district, though it is not as a rule so abundant as *zaddachi* and does not penetrate as far into the more diluted waters. Thus *locusta* on the Finnish coasts is confined to the south-west waters with a minimum salinity of *c.* 5–6 °/₀₀ (see Fig. 6). *G. locusta* is also missing in the Swedish samples from the waters off Stockholm to Kalmar. The depth in the places of capture generally does not surpass a few metres; in the material from the open and comparatively deep waters between Rügen and the Danish Isles, where *zaddachi oceanicus* and *salinus* occur commonly, the species is practically missing.

The samples from the Cattegat contain *locusta* in much greater numbers than *zaddachi*, and in the collections from the west coast of Denmark only the former species is present.

Summary of the Gammarus *fauna of the Baltic.* The forms treated above are the only common species of *Gammarus* of this area. Besides them the area seems to harbour only *G. duebeni*, which is confined to very shallow water and to special localities (it occurs mainly in brackish rockpools and similar small basins on the shore of islands, exposed to the sea; see Segerstråle, 1946). There is no evidence for the occurrence of *G. setosus* Dement. Dementieva's *G. setosus* f. *baltica* and Dahl's *G. locusta* f. *setosus* from Baltic localities are attributed to *G. z. zaddachi* (see synonyms, p. 231).

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[1] The Danish collections include, amongst other, the material used by Blegvad for his investigation on the biology of *G. locusta* (1922). Of *c.* 210 specimens from this collection, examined in connexion with the present investigation, *c.* one-third (70 specimens) proved to belong to this species, the rest being *G. zaddachi oceanicus*, and *salinus*. This result is by no means surprising in view of the confusion prevailing especially in earlier years. Blegvad also observed that the specimens studied by him varied greatly.

Randers Fjord

A comparatively large collection of *Gammarus*, made by Johansen and Ussing during their investigations of the invertebrate fauna of this water, situated on the north-east coast of Jutland in Denmark and interesting because of the decreasing salinity from the mouth to the more inland parts, is discussed in Stephensen's paper of 1917. He records the following species and forms from the area: *G. locusta*, *G. locusta* var. *Zaddachi*, an intermediate form between *G. locusta* and this form, as well as *G. duebeni* and *G. pulex*. Later on, in 1927, Stephensen identifies some of the intermediates between *G. locusta* and *G. locusta* var. *Zaddachi* as *G. duebeni*. The material concerned was deposited in the Museum of Copenhagen, and all of it, excepting that of *G. pulex* and *G. duebeni*, was kindly sent by Mr Stephensen to the author, who has thus had the opportunity of going through it.

The results are as follows. Most specimens labelled *G. locusta* are correctly determined (one being an intermediate between the subspp. *oceanicus* and *zaddachi* of *G. zaddachi*). The form called *G. locusta* var. *Zaddachi* is mainly *G. z. zaddachi*, whereas the 'intermediate form between *G. locusta* and *G. locusta* var. *Zaddachi*' includes all three subspecies of *G. zaddachi*; in addition, there are some *G. locusta* and one *G. duebeni* (this species captured at St. 9, depth 0 m.). In a number of samples of *G. zaddachi*, the subspecies could not be determined, on account of the very small size of the animals. The study of the material has given the following ranges of distribution:

G. zaddachi zaddachi:	St. 2 (salinity from 1–2 to 12 $^{\circ}/_{\circ\circ}$)
oceanicus:	St. 8–10 (salinity from 5 to at least 24 $^{\circ}/_{\circ\circ}$)
G. locusta:	St. 10 (salinity from *c.* 17 to at least 24 $^{\circ}/_{\circ\circ}$).

As seen from the above records the subspecies of *zaddachi*, as well as *locusta*, follow one another in the same order as in the Baltic area. The salinities at the most inland localities for *z. oceanicus* and for *locusta*, are higher in Randers Fjord than in the Baltic, but this phenomenon is obviously due to the comparatively scanty material from the Fjord.

Ringköbing Fjord

This water, located on the west coast of Jutland, is connected with the North Sea through only a narrow opening. The water is consequently brackish, the (surface) salinity averaging in the main part of the area *c.* 4–8 $^{\circ}/_{\circ\circ}$. The

Gammarus fauna has been treated by Poulsen (1933–6). He records the following species: *G. locusta*, occurring only in the very opening of the Fjord; *G. duebeni*, common everywhere, excepting in the saltest part, and observed also in the lowermost course of the river Vondaa; *G. zaddachi*, found only in a small basin, which is separated both from the Fjord and from the North Sea.

Fortunately, the collection received for the present investigation from the Copenhagen Museum includes about forty samples of the Ringköbing Fjord material (the determination, however, is not given on the labels), thus enabling the author to check the records which were given by Poulsen and of which some appeared doubtful.

The results are as follows. (1) The main *Gammarus* of the Fjord is not *duebeni*, but *zaddachi*. All the specimens of this species, which are large enough to be identified, belong to *z. zaddachi*. *G. duebeni* is certainly present in the material, but occurs only in a few samples, all taken in very shallow water (0–0·5 m.). The localities are: the mouth of the River Vondaa; near the bridge in this river; off Gammelsogns Mölle; on the shore *c.* 200 m. east of the mouth of the River Falen; Gjödel Canal, near the bridge at Lönne Klit.

(2) *G. z. zaddachi* occurred in different parts of the Fjord, from the shore to open areas with depths of *c.* 3 m. (maximum depth of the area *c.* 6 m.). In addition, one sample has been collected in the mouth of the River Vondaa, near the bridge (3 July 1921).

(3) The true *locusta* was found only in one sample (Söndre Dyb, 3·5 m.). Poulsen records the species from the saltest parts of the Fjord. These samples are lacking in the material available to the present author, but as the characteristics given for this species by Poulsen are quite correct there is no reason to doubt these determinations.

(4) The '*G. zaddachi*' mentioned in Poulsen's paper seems not to be included in the preserved material, but the illustrations given suggest that the form of the species in question is *oceanicus*.

THE RELATIONSHIP BETWEEN *GAMMARUS ZADDACHI* AND THE SPECIES *G. SETOSUS* AND *G. WILKITZKII*

In the material from the Arctic there are numerous samples containing the large species *G. setosus* and *G. wilkitzkii* (many of the samples are labelled *G. locusta*), thus enabling the author to compare them with *G. zaddachi*.

G. setosus (material: about thirty-five samples from Arctic Canada, Greenland, Iceland, Spitsbergen, east coast of Murman, Novaya Zemlya, Kara Sea, the Arctic Sea off Siberia). This species was separated from *G. locusta* and established as an independent species by Dementieva (1931), mainly on material from Arctic waters (the amphipod regarded by this author as a Baltic form of *setosus* is obviously identical with *G. z. zaddachi*). Stephensen

(1940) records it as *G. locusta* subsp. *setosus*, and gives the first accurate description of the form.

The examination of the specimens in the present material showed that the species is as little allied to the true *locusta* as is *zaddachi*, but there is a close relation between *setosus* and the last-mentioned species, especially subsp. *oceanicus*. As in *zaddachi* the head sinus is deep, the 4th side-plate has the same semicircular lower margin, the pleon epimera show no difference in shape, the last uropods have the inner ramus of the same relative length, and as to the relative length of the peduncle of antenna 1 there is a strict agreement with *zaddachi oceanicus*.

The main differences are as follows. (1) The common occurrence of plumose setae in *setosus*, particularly on peraeopods 5–7 (segments 4–6), pleon segments 4–6, and the telson; here practically all the setae are feathery (cf. Stephensen, 1940, fig. 41). In addition the apical hairs on the telson are markedly longer than in *z. oceanicus* (in the male about three times as long as the corresponding spines (or longer), against at most about twice the length in *z. oceanicus*). (2) The 2nd and 3rd peduncle segments of antenna 1 bear hair clusters, on the under side, from 5 to about 7, and 2–3 respectively, whereas *z. oceanicus* has 3–5 and 1–2 respectively. (3) The eyes are generally distinctly smaller in *setosus*. (4) The 2nd gnathopod in this species is as a rule considerably stouter and its hind margin much more bulging; besides, the gap between the mid-palm spine, present in the male, and the palmar-angle spine-row is usually far less pronounced (Fig. 7) (in addition, in the female the latter spine group occupies a greater part of the palma in *setosus* than in *z. oceanicus*).

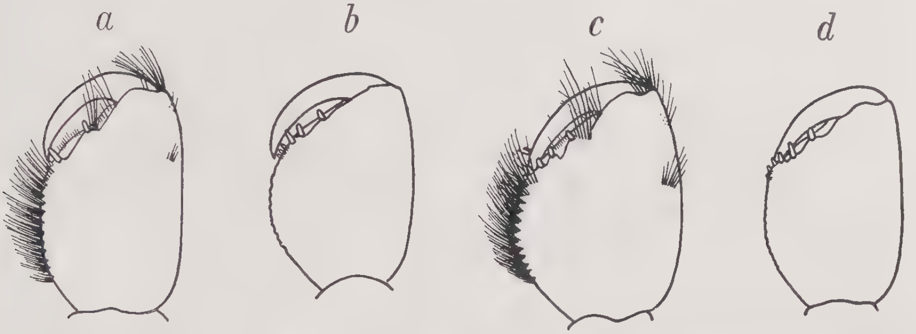

Fig. 7. Second gnathopods of *Gammarus zaddachi oceanicus* (*a*, *b*) and *Gammarus setosus* (*c*, *d*) (males) to show variation in shape. *a*, *oceanicus*, typical (Murman Coast, body length 30 mm.). *b*, *oceanicus*, approaching typical *setosus* (Spitsbergen, 25 mm.). *c*, *setosus*, typical (east Greenland, 32 mm.). *d*, *setosus*, approaching typical *oceanicus* (the Arctic Sea off Siberia, 26 mm.). In *b* and *d* the setae are omitted.

According to the author's observations only the characteristics mentioned above under (1) always separate *setosus* from *zaddachi oceanicus*, whereas, when comparing the former species with large specimens of *oceanicus*, the other characteristics may overlap more or less (Fig. 7). Even in the occurrence of feathery setae there may be some transition, *oceanicus* occasionally having single plumose hairs on the last uropods, pleon segments, and telson (Fig. 3 *f*), but the difference is nevertheless very marked.

Besides *G. setosus*, the very large Arctic species *G. wilkitzkii* (length up to 48 mm.; Gurjanova, 1930) is closely allied to *zaddachi*. It has even been reported by some writers, amongst others Stephensen, as possibly being identical with this species. In fact, the differences between *z. zaddachi* and *wilkitzkii* are small.[1] They seem, however, to be great enough to justify retaining the latter as an independent species, as suggested by Sexton (1942). The same conclusion appears to hold good regarding *setosus*. If these two forms were considered subspecies of *zaddachi*, the still closer relation between the subspecies *zaddachi*, *oceanicus*, and *salinus* would not be so clearly seen. But it seems natural to let them constitute—possibly together with some other species, less thoroughly known by the author—an independent group within the subgenus of *Gammarus* proper, and naming this group after the species *zaddachi* is suggested. Most of the principal characteristics which distinguish the members of this group from *G. locusta* are the same as those summarized on p. 220; to them should be added the differences in the shape and spinose armature of gnathopod 2.

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[1] The following divergence observed in material investigated by the author may be added to those listed by Sexton (1942). The peduncle of antenna 1 is still longer than in *z. zaddachi*, viz. as long as the distance from tip of rostrum to hind margin of peraeon segment 2; in *z. zaddachi* the peduncle reaches at the most to the middle of the said segment.

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THE STRUCTURE, TADPOLE AND BUDDING OF THE ASCIDIAN *PYCNOCLAVELLA AURILUCENS* GARSTANG

By N. J. Berrill

From the Plymouth Laboratory and McGill University, Montreal

(Text-figs. 1–3)

Pycnoclavella aurilucens was recorded and briefly described by Garstang in 1891 from a limited locality in the Plymouth area, and has not been found with certainty of identification from any other region. There has been a tendency to subordinate it as a species of *Clavelina*, but the dissimilarities are greater even than the original description implies and this procedure is not justified. The genus is accordingly retained, and a more detailed account of the colony, with the first description of the tadpole larva and process of budding, is presented.

Colonies are usually found growing on gorgonians, large hydroids and calcareous algae at depths of 25–30 m. associated with coarse shell gravel and polyzoa such as *Lepralia*. It is known to occur only in the Plymouth region, unless the form known as *Clavelina nana* reported from Roscoff and Banyuls (Giard, 1873, Lahille, 1890) turns out to be identical with it. The external appearance of the colonies and of the constituent zooids has been well described by Garstang in the second volume of this *Journal*. In brief, the colonies are encrusting, the thoracic parts of the small delicate zooids extending freely from a greenish matrix in which the abdomens are embedded. The endostyle and peripharyngeal bands are picked out in yellow or white pigment and are very striking; the zooids are very contractile.

STRUCTURE OF THE ZOOID

The zooids (Fig. 1) in general structure are much like those of *Clavelina*. They are much smaller and consequently have a less elaborate branchial sac, there being seven rows of gill-slits, rarely eight or nine. The endostyle is comparatively massive, as noted by Garstang, and the siphons independent and without lobes as is in other members of the Clavelinidae. Dorsal languets, corresponding in number to the rows of stigmata, occur along the dorsal line of the branchial sac. The oesophagus is long, the stomach squarish in cross-section as in *Clavelina* and leading into a typical post-stomach, the latter in turn connected with the intestine proper by a vertically aligned mid-intestine. The rectum opens into the atrial cavity level with the most posterior row of

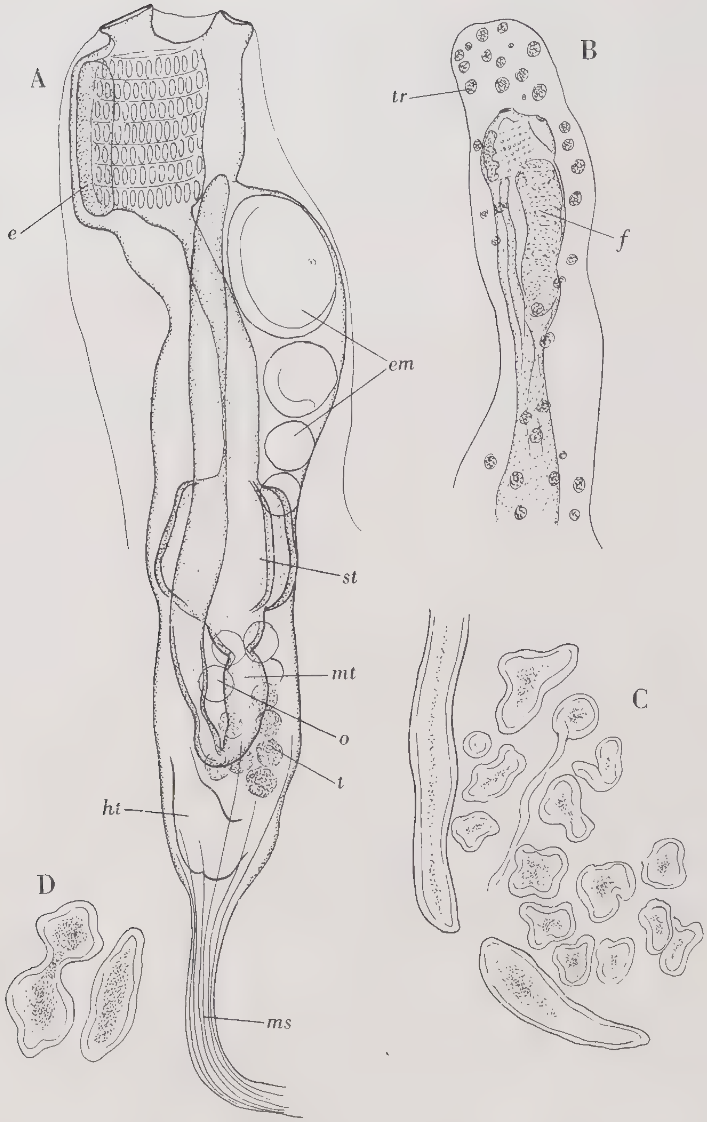

Fig. 1. A, mature zooid of *Pycnoclavella*, with ventral stolon incomplete and embryos developing within oviduct. B, zooid undergoing resorption after end of sexual breeding phase, with large 'trophocytes' accumulating in test. C, distal end of ventral stolon showing separation of ampullary bud chambers and fragmentation of stolon stem. D, isolated buds from another part of colony. *e*, endostyle; *em*, embryos; *f*, faeces trapped in resorbing intestine; *ht*, heart; *ms*, muscle fibres in ventral stolon; *mt*, mid-intestine; *o*, ovary; *st*, stomach; *t*, testis; *tr*, trophocyte.

gill-slits. The heart lies posterior to the loop of the digestive canal, and is virtually straight. The epicardium extends throughout the length of the abdomen in a fused condition, its double nature indicated only by a shallow bilobed condition at its posterior extremity level with the bend of the gut-loop, and anteriorly as a pair of horns ending blindly just beneath the branchial sac from which it arises during development.

As in *Clavelina* there is a prolonged post-abdominal extension of the body wall in which the longitudinal retractor muscles are included. Other structures or organs do not extend into this stalk or stolon, so that it is not a post-abdomen of the kind encountered in the Synoicidae. Posteriorly the stolon tends to branch and processes may be reflected along the sides of the abdomen.

The gonads lie posterior to the stomach alongside the posterior part of the gut-loop. Both the sperm duct and oviduct open at the base of the atrial cavity. The oviduct is wide and eggs are fertilized while within it, early cleavage stages occurring near the level of the stomach and later stages up to the mature tadpole larva being found more anteriorly.

Budding

The process of budding is apparently essentially similar to that of species of *Clavelina*. The posterior end of the post-abdominal stolonic extension branches and breaks up into ampullary chambers, somewhat larger fragments arising from fragmentation of the main stalk. These pieces consist of a layer of epidermis of irregular form, and contain mesenchymatous tissue that served originally as part of the mesenchymatous septum separating the afferent and efferent blood flow in the stolon. Actual separation of a united ampullary cluster into isolated fragments appears to be mainly a phenomenon of early or mid-winter, and development into new zooids never takes place while tissue continuity is retained with the parent zooid.

Nutrition of a bud appears to be somewhat different from that of *Clavelina* proper, though it is none too well known and neither is the development of the bud itself. There is clearly some concentration of reserve food cells within the bud fragments, but not to a comparable degree, and it is possible that the medium of the common matrix external to the buds may become nutritional as in *Distaplia*. In any event, as the zooids of a colony begin to resorb after the close of the sexual breeding phase, cells lying within or migrating into the thoracic and abdominal tunic become greatly enlarged and closely resemble the trophocytes of other forms, and such cells together with other dissolution products undoubtedly comprise the entire source of nutrition for the buds in *Distaplia* colonies. The process of resorption follows an orderly course and the reduction of structures and tissues is in general like that described for *Clavelina* by Huxley (1926).

DEVELOPMENT AND STRUCTURE OF TADPOLE

The egg is comparatively yolky and as such is relatively small, of about 0·28 mm. diameter (Fig. 2A). Fertilization occurs at the base of the oviduct by sperm entering from the atrial chamber. The pattern of early cleavage is not known, though in the equally yolky eggs of *Amaroucium* (Scott, 1945) the basic pattern established by Conklin (1905) for the smaller eggs of *Styela*, *Ciona* and *Phallusia* is not significantly affected. During embryonic development there is considerable growth, the trunk of the tadpole exclusive of the tail having a length several times the diameter of the egg.

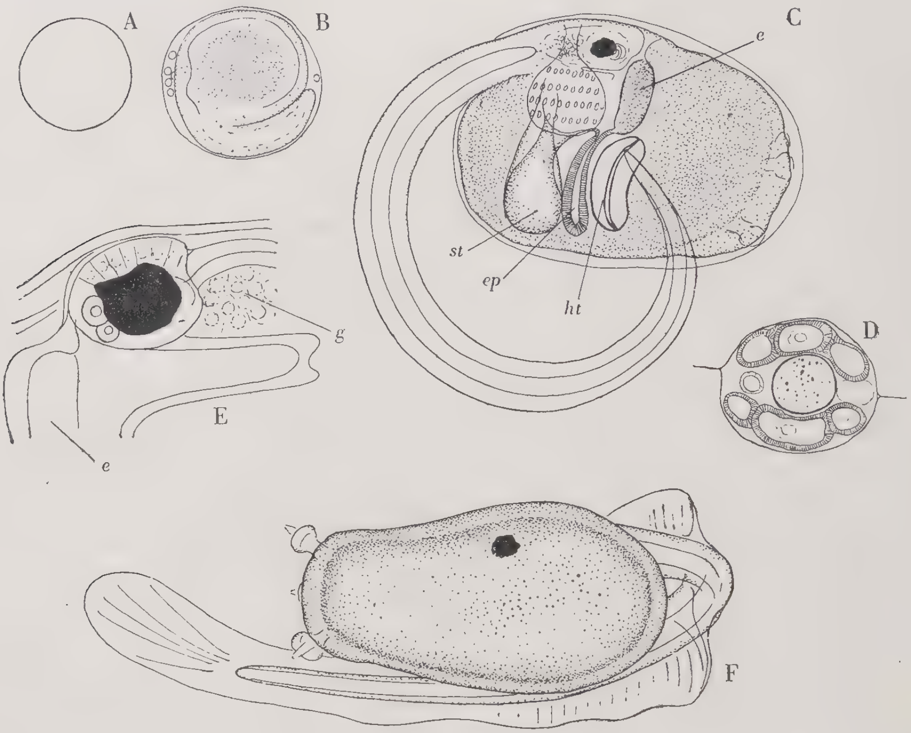

Fig. 2. *Pycnoclavella*, development of tadpole. A, egg. B, embryo within membrane. C, tadpole near time of liberation, all drawn to same scale. D, cross-section through horizontally twisted tail showing central notochord cell and lateral bands of muscle cells. E, sensory vesicle of tadpole at higher magnification, showing absence of otolith and presence of large mass of ocellus pigment together with two spherical lens cells. F, fully developed tadpole drawn from living specimen. *e*, endostyle; *ep*, epicardium; *g*, ganglion; *ht*, heart; *st*, stomach.

At the time of liberation of the tadpole the trunk is greatly distended and the permanent ascidian structure contained within is considerably advanced

(Fig. 2C). The tail is large and well developed, having a broad cuticular fin throughout its length and extending as a blade beyond, the whole being twisted through 90°, as in all ascidian tadpoles developing from large or yolky eggs excepting those of the *Pleurogona* (Ptyochobranchia). Muscle tissue lies on each side of the central notochord as a band three cells wide (Fig. 2D). The notochord itself consists of about 40 cells. The free-swimming period of the few living tadpoles studied lasted approximately 1 hr., a period consistent with the very local and selective habitat of the species. At 18° C. the stroke of the tail was 25–30 per sec. and the speed about 3 mm. per sec.

The trunk of the living tadpole (Fig. 2F) is a dense green and the internal organs hard to distinguish. The green colour is due to enormous numbers of peculiar bladder cells congesting all internal space not otherwise occupied. There are three typical adhesive organs at the anterior end, each with a stalk deeply invaginated. Of the larval organs *per se* the sensory vesicle is unique. While a number of ascidian tadpoles are known with only an otolith but no ocellus, *Pycnoclavella* alone of those so far examined has an ocellus but no otolith (the Thaliacean condition is not relevant to this discussion). The vesicle (Fig. 2E) is not noticeably abnormally small, yet it contains no trace of an otolith while the ocellus itself is a little unusual. The mass of pigment is relatively large although the associated retinal cells do not appear to be correspondingly numerous. The lens cells, however, which are three in the great majority of ascidian tadpoles, are here represented only by two.

As in most yolky ascidian eggs, the development of the larval (tadpole) structure is relatively retarded, probably as in other forms due to the slow differentiation of yolk-laden notochord cells (cf. Berrill, 1935*a*, *b*). Accordingly the permanent ascidian structure is relatively well developed within the active tadpole, and lies mainly in the posterior half of the trunk with the axis vertical to the long axis of the tadpole. The mouth is formed though not functionally open, and the pair of peribranchial sacs that appear independently on each side at an earlier stage are fused dorsally to form the atrial aperture. The endostyle is short and thick. Adjacent to it on each side the peribranchial sac is perforated by four rows of definitive stigmata, with nearly the same number per row as in the mature zooid. In the ventral part of the trunk, the pharynx opens into the oesophagus and stomach, the digestive canal as a whole forming a vertical U-shaped tube. Immediately in front of the oesophageal opening and behind the base of the endostyle, a second outgrowth extends ventrally from a pair of initial evaginations from the floor of the pharynx to form the epicardium. It later loses its connexion with the pharynx. Anteriorly to the epicardium and ventrally to the endostyle, but not connected with either, lies the large pericardium and heart.

Postlarval Development

After settling the tail is rapidly absorbed, complete absorption taking not more than an hour. After about 12 hr. (at 18° C.) the tail consists of a compact, more or less spherical, mass of cells attached to the posterior end of the trunk; the adhesive organs no longer are recognizable, and at the anterior region three large epidermal outgrowths appear (Fig. 3A). The rate of further development is somewhat variable, the permanent organs still being in a non-functioning state 3 days later, but after 5 days varying from an inactive condition to one in which the heart, siphons and gill-slits are all fully functional (Fig. 3B, C). At this time the thorax has become transparent and virtually colourless, except for a pair of prominent pigment patches, one on each side of the pharynx in front of the most anterior row of stigmata. The abdomen is greatly elongated, and dense with the green cells noted in the tadpole. The heart now lies at the base of the abdomen. Of the three epidermal outgrowths, one usually continues to grow and the others shrink. At the end of two weeks (Fig. 3D) little further change has occurred, at least under laboratory conditions, the only obvious growth being that of a sheet of tunicin, richly impregnated with small brown cells, over the substratum.

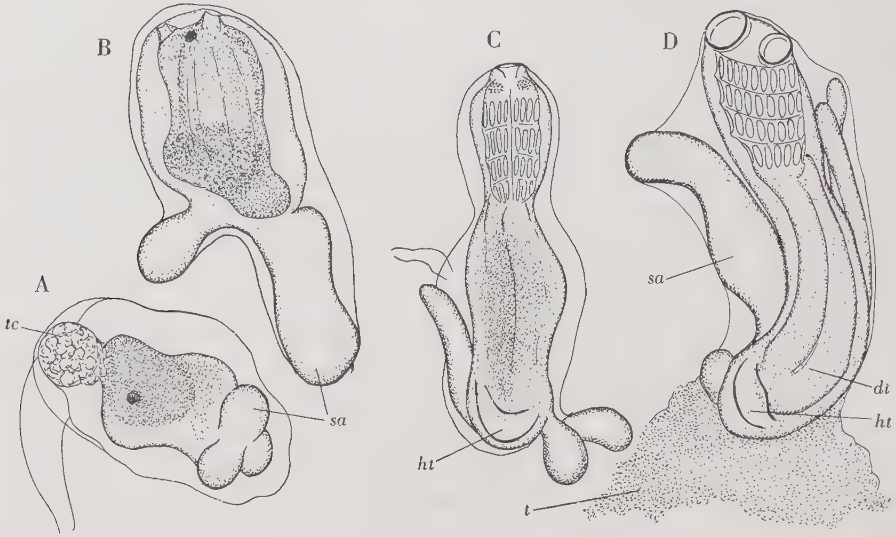

Fig. 3. *Pycnoclavella*, metamorphosis and post-larval development (at 18° C.). A, 12 hr. after attachment with tail absorbed and anterior ampullae growing. B, C, 3–5 days later, showing abdominal extension, further growth of ampullae, and formation of active gill slits. D, individual two weeks after attachment with sheet of test substance growing over substratum. *dt*, digestive tube; *ht*, heart; *sa*, stolonic ampulla; *t*, test substance; *tc*, mass of tail cells.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

Untersuchungen über die Eiweissverdauung *in vivo* und *in vitro* bei einigen Gastropoden

By **Greta Hörstadius**, geb. **Kjellström**, und **Sven Hörstadius**

Pubb. Staz. Zool. Napoli, Vol. 18, 1940, pp. 151–249

The digestion of proteins was studied in some marine Gastropoda, and the results that refer to work performed at The Marine Biological Laboratory, Plymouth, are as follows:

In *Hermaea dendritica* phagocytosis was with certainty shown to occur in the 'liver' by feeding the animals with algae containing chloroplasts of different size (*Bryopsis* and *Codium*). In the ingested chloroplasts the characteristic starch reaction could be demonstrated.

In *Pleurobranchaea meckeli* phagocytosis was proved with gold fibrin as well as with carmin, in *Archidoris britannica* with gold fibrin (visible colloidal gold particles embedded in fibrin).

In the carnivore *Pleurobranchaea meckeli* the juice in the crop hydrolyzed casein at *p*H 5·5, fibrin at 7, gelatin and pepton-Witte at 7. Glycyl-glycin was not hydrolyzed at *p*H 7·5. Extract of the digestive diverticula (liver) hydrolyzes the same substrates as the juice of the crop, and also glycyl-glycin. The strength of the enzymes in the crop shows during the first 10 hr. after feeding a maximum after 3 hr. The dipeptidases do not vary in strength. The juice is very active on Spritblaufibrin, but the extract is inefficient, although both of them hydrolyze casein and gelatine equally. S.H.

Resting and Action Potentials in Single Nerve Fibres

By **A. L. Hodgkin** and **A. F. Huxley**

Journ. Physiol., Vol. 104, 1945, pp. 176–95

A technique for introducing micro-electrodes into the interior of a giant axon from *Loligo* is described. The axon was stimulated electrically and direct measurements of the action potential and resting potential were made with an amplifier and oscillograph. Experiments with external electrodes showed that the action potential was conducted for at least a centimetre beyond the tip of the micro-electrode and that the introduction of a micro-electrode had no effect upon the ability of the nerve to conduct impulses. The absolute magnitude of the action potential and resting potential are given as about 90 and 45 mV.

Measurements with external electrodes show that the action potentials of *Homarus* and *Carcinus* nerve fibres are also much larger than the resting potential.

These results have an important bearing on theories of nervous conduction. They show that classical physiologists were right in thinking that electrical changes originate at the surface membrane of a nerve fibre, but were wrong in believing that the action potential arose solely from a breakdown of the pre-existing resting potential.

The experiments described in this paper were completed in 1939 but the outbreak of war delayed publication of a full account of the results until 1945.

A.L.H.

The Neurological Basis of the Locomotory Rhythm in the Spinal Dogfish (*Scyllium canicula*, *Acanthias vulgaris*).
I. Reflex Behaviour

By **H. W. Lissmann**

Journ. Exp. Biol., Vol. 23, 1946, pp. 143–61

The idea that rhythmically co-ordinated movements of animals are driven and governed by an automatic mechanism within the central nervous system has been steadily gaining ground. Previous research on the dogfish led to the conclusion that the persistent locomotory rhythm, characteristic of spinal preparations, arises from bursts of motor impulses emanating spontaneously from the central nervous system, and is not essentially dependent on afferent stimulation.

The present investigation of body and fin reflexes makes it difficult to accept this picture for the following reasons. (i) If swimming is induced in inactive preparations through a localized exteroceptive stimulus, the position of the initial swimming posture depends solely on the site of stimulation. (ii) Diffuse touch to the ventral surface of a spinal preparation inhibits the swimming movements. Some dogfish remain immobile after the inhibitory stimulation has been discontinued, but they resume their persistent swimming on application of a single excitatory stimulus. (iii) Through feeble transitory stimuli any individual swimming stroke can be retarded, temporarily arrested, reversed, accelerated and augmented. The reaction depends on the site of stimulation and on the momentary phase of the swimming movement at which it is applied. The rhythm emerging after the application of a transitory stimulus is, as a rule, out of phase with the rhythm as recorded prior to the application of the stimulus.

H.W.L.

THE NEUROLOGICAL BASIS OF THE LOCOMOTORY RHYTHM IN THE SPINAL DOGFISH (*SCYLLIUM CANICULA*, *ACANTHIAS VULGARIS*).
II. THE EFFECT OF DE-AFFERENTATION

By **H. W. Lissmann**

Journ. Exp. Biol., Vol. 23, 1946, pp. 162–76

The persistent swimming rhythm, typical of a spinal dogfish, is completely abolished as soon as all afferent excitation is cut off by severance of all the dorsal roots. The rhythm still emerges clearly when about half the number of the dorsal roots is transected, irrespective whether the anterior or the posterior half of the animal be de-afferentated, or whether complete unilateral de-afferentation is performed. Extensively de-afferentated preparations may exhibit swimming movements only after exteroceptive stimulation or after electrical stimulation applied directly to the spinal cord; these swimming movements do not persist. If only a small patch of the body surface remains sensitive, then, on stimulation of this region, the preparation exhibits a static reflex posture.

No evidence has been found to support the view that the locomotory waves of the spinal dogfish result from a spontaneous and automatic activity in the central nervous system; the experimental findings suggest that the locomotory waves can be essentially considered as moving sites of nervous integration, and that peripheral stimulation plays a fundamental role in this process.

H.W.L.

RELATIVE GROWTH OF THE EUROPEAN EDIBLE CRAB, *CANCER PAGURUS*.
III. GROWTH OF THE STERNUM AND APPENDAGES

By **Donald C. G. MacKay**

Growth, Vol. 7, 1943, pp. 401–12

The results of a study of form changes in the European edible crab, *Cancer pagurus*, have been analysed by Huxley's method and have been presented in three papers of which this is the third and final one. The study was carried out at the Marine Biological Laboratory at Plymouth during the year 1934–5.

The results of the study indicate that males and females differ only slightly in the growth of the sternum. In male crabs, both immature and mature, the appendages studied display positive heterogony. In females the chelae are positively heterogonic, the walking legs negatively so. The growth coefficient is higher for the chelae of mature males than for immature ones. Growth changes are such as to produce larger chelae and longer legs in males than in females of corresponding carapace length.

Altogether twenty-six body measurements were studied. The highest growth coefficients in males were found for the chelae of immature crabs (for length, $k=1\cdot48$; for width, $k=1\cdot40$). For females the highest growth coefficient was found for the 4th abdominal segment of adults ($k=1\cdot50$).

In general, *C. pagurus*, like *C. magister* which had been studied previously, shows a low degree of heterogony and consequently is able to grow to a considerable size (10–12 lb.) without marked changes in the form of the body.

D.C.G.M.

THE DETERMINATION OF THE DEPTHS AND EXTINCTION COEFFICIENTS OF SHALLOW WATER BY AIR PHOTOGRAPHY USING COLOUR FILTERS

By J. Grange Moore

Phil. Trans. Roy. Soc. Lond. A, Vol. 240, pp. 163–217

Submerged beaches viewed vertically from the air vary in apparent brightness with the depth and effective extinction coefficient of the water. If one be known, the other may be calculated from sensitometric measurements on a single air photograph taken through a suitable filter.

If neither be known, a pair of photographs is taken simultaneously through contrasting filters; in average coastal water and with suitable photographs, depths exceeding 20 ft. may then be determined with an error of less than ± 10%, by making use of a general relationship between extinction coefficients at any two given wavelengths; from these depths extinction coefficients may then be calculated.

The theoretical and practical details, the limitations and uses of the method, and the results obtained during a year's work over Cornish and Mediterranean beaches and elsewhere, are described and illustrated. Records for interpretation by oceanographers, marine surveyors and engineers can rapidly be obtained over large areas of coastline.

J.G.M.

LABORATORY REGULATIONS

At a Council Meeting, held on 12 April 1947, the regulations with regard to the admission of visiting workers to the Plymouth Laboratory were amended as follows:

1. Any Governor or Founder of the Association is entitled to occupy personally a table at the Plymouth Laboratory without payment. A Governor or Founder shall have the privilege, upon signifying to the Director his intention to forgo in any year the right of personally occupying a table in the Laboratory, of nominating an eligible person to make use of a table for one month in that year free of charge.

2. The charge for a table shall be 50 guineas a year, 5 guineas a month, and £1. 10*s*. a week, to be paid in advance.

3. Members of the Association have the first claim to become renters of tables, and shall have the privilege of occupying a table for one week in each year free of charge.

4. The Council of the Association may remit, in whole or in part, the payment of rent for a table in special cases.

5. Applications from Members and others desiring to occupy tables must be made in writing to the Director, and a notice of at least seven days will be expected before any table is ready for use.

6. The Association undertakes, so far as possible, to supply the material required for any investigation, and such facilities for obtaining and working with it as may be at the command of the Association. No visiting worker can be permitted to make biological collections in the Laboratory. The Association undertakes to supply collections of marine animals and plants at a fixed price to those who wish to buy them. This rule must be understood to apply only to general biological collections. Visiting workers are at liberty to collect and take away with them any material that is necessary for the prosecution of their research on payment of the cost of microscope slides, cover-slips, glass tubes, expensive reagents, bottles and packing cases necessary for its removal.

7. Visiting workers are expected to furnish the Director with a summary statement of the published results of investigations carried on by them in a form suitable for publication in the *Journal* of the Association.

8. Visitors working in the Laboratory will have free access to the tank-room, but they are not permitted to have access to the interior of the tanks without the permission of the Director. Facilities for conducting experiments on a large scale will be granted as far as space permits.

9. The Director has control over the Laboratory, boats, equipment and apparatus of the Association. Visiting workers are admitted on condition that they accept this control, and agree to abide by the regulations drawn up by the Council of the Association.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1946–47

The Council and Officers

The Council have to report with regret the death of two Vice-Presidents of the Association during the year: Lord Mildmay of Flete, P.C., a Vice-President since 1939, and Sir Joseph Barcroft, F.R.S., who served for many years as an active member of the Council and was also an Associate Member.

The following changes have been made in the Annual Governors during the year. Mr P. D. H. Dunn, C.M.G., O.B.E., has been appointed as representative of the Ministry of Agriculture and Fisheries on the resignation of Mr A. T. A. Dobson, C.B., C.V.O., C.B.E. The new Prime Warden of the Fishmongers' Company is Mr Benjamin Travers, A.F.C. Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O., has resigned as an Annual Governor representing the Fishmongers' Company. The Council wish to record their appreciation and thanks for the great services rendered to the Association by Mr A. T. A. Dobson and Admiral Sir Aubrey Smith.

Four ordinary meetings of Council were held during the year, two in the rooms of the Royal Society, one in the rooms of the Linnean Society and one at Plymouth. At these the average attendance was 14. The Association is indebted to the Councils of the Royal Society and the Linnean Society for the use of their rooms.

The Plymouth Laboratory

During the year all remaining minor repairs necessary to complete the restoration of the Laboratory have been finished, except in the centre block of the main building for which certain materials are still awaited. The outside tank destroyed by the bombing has been rebuilt and a new outside circulation bench constructed. Much needed painting to the exterior of all buildings has been done.

A grant has been sanctioned by H.M. Treasury towards the rebuilding of the Director's House as laboratory accommodation, and the work has now been started.

A small building on the pier at Newlyn, in Cornwall, has been rented by the Association for use as a temporary laboratory in which samples of fish or material collected in the research ship while cruising in the vicinity can be dealt with. It is essential, for instance, that there should be the least possible delay in certain chemical analyses of water samples after their collection.

Aquarium

During the year the repairs to the aquarium were completed and the tank room was reopened to the public on 5 November 1946, by the Lord Mayor of Plymouth, the Rt. Hon. Isaac Foot, P.C. The opportunity has been taken to rebuild the rockwork using local wave-worn boulders from the beach. The work has been done by laboratory staff under Mr D. P. Wilson's supervision. The finished product is generally considered to be a great improvement, both artistically and as representative of the natural surroundings; this it owes especially to the skill of Mr F. G. C. Ryder. Screens have also been erected to improve the lighting and viewing of the main tanks.

Over 4000 members of the public visited the aquarium during the first fortnight after it was reopened, and a good attendance is being maintained. Parties of school-children are again making use of the educational facilities afforded.

The Ship and Motor Boat

The 90-ft. motor fishing vessel (M.F.V. 1564) chartered from the Admiralty, and now registered as Research Vessel *Sabella*, was handed over to the Association on 29 May 1946. The vessel was built by the Wivenhoe Shipyard Ltd. at Wivenhoe, Essex, and Mr G. A. Steven gave much time and attention to supervising the alterations necessary to fit her for scientific research purposes. Mr Steven was present at the trials off Brightlingsea on 28 May, and he accompanied her on the trip to Plymouth where she arrived on 1 June. After a spell in harbour necessary for fitting out with research and fishing equipment she went into service on 13 June. Since then she has been in continuous commission and has proved in most respects highly satisfactory for the work. Her captain is Skipper W. J. Creese, who before the war was mate on the *Salpa*.

The motor boat *Gammarus* has worked throughout the year. In September 1946 she was given a major overhaul by the original builders. The hull and woodwork are in excellent condition, and the boat should be fit for many more years' service.

The *Salpa* has not yet been released by the Ministry of Transport, but the off-survey is in progress.

Government Surplus Equipment

Through the help of the Development Commissioners the Association has obtained a 10 h.p. Hillman army utility van. This is proving most serviceable for carrying material from the ship and for collecting purposes.

Full opportunity is being taken of the facilities offered by the Ministry of Supply and other departments for obtaining equipment and apparatus from government surplus disposal stores. Dr W. R. G. Atkins and Mr F. J. Warren have spent much time on the selection of material and as a result the laboratory is becoming very well stocked with electrical fittings and other equipment useful for research purposes. The workshop is also now well equipped with machine and other tools.

The Staff

Mr P. G. Corbin was appointed to the staff of the Plymouth laboratory as Scientific Officer as from 1 January 1947. Prior to that date he had been working at Plymouth since 7 May 1946, with a grant from the Ministry of Agriculture and Fisheries for the completion of the mackerel investigations made before the war.

Mr H. G. Vevers, M.B.E., has been appointed Administrative Bursar on the scientific staff of the Plymouth laboratory. He joined the staff on 1 June 1946, and has given very great assistance in the administrative work necessary to put the laboratory on a peace-time footing.

Dr J. F. Danielli resigned from the post of Physiologist in the autumn of 1946 on his appointment to a Readership in Cell Physiology in the University of London tenable at the Royal Cancer Hospital.

Mr G. A. Steven was promoted to Principal Scientific Officer as from 1 October 1945; and Dr L. H. N. Cooper and Mr G. M. Spooner were promoted to Senior Scientific Officers as from 1 October 1945, and 1 April 1946, respectively.

Mr A. D. Mattacola resumed his duties on the technical staff on 27 May 1946, after war service with the Royal Tank Corps.

Mr A. G. Butler, the Assistant Caretaker, retired in October 1946, after nearly 27 years of faithful service to the Association.

Mr F. S. Russell and Dr H. W. Harvey attended the thirty-fourth meeting of the International Council for the Exploration of the Sea at Stockholm in August 1946.

Members of the staff have attended a number of meetings of scientific societies during the year, including the Joint Meetings of the Challenger Society and Representatives of Marine Laboratories which have now been resumed.

Dr W. R. G. Atkins and Dr H. W. Harvey have continued their work on the Marine Corrosion Committee of the Iron and Steel Institute.

On 6 March 1947 Mr F. S. Russell delivered a lecture to the Royal Society on the Plymouth Laboratory; this was the first of a series of lectures to be given at the Royal Society on British laboratories.

During the Michaelmas term 1946, Mr T. R. Tozer of the technical staff spent six weeks in the Zoological Department at Cambridge gaining experience in laboratory technique.

Occupation of Tables

The following seventy-two workers have occupied tables at the Plymouth Laboratory during the year:

B. C. Abbott, London (General biology and histochemistry).
C. W. M. Adams, London (Study of Ascidians and Tunicates).
Dr C. Amirthalingam, Ceylon (Library).
Miss E. Batham, Cambridge (Nerve-net of Actinozoa).
Dr Anna Bidder, Cambridge (Digestive mechanism of *Loligo*).
Miss C. H. Brown, Cambridge (Skeletal proteins of Invertebrates).
D. A. Brown, New Zealand (Polyzoans).
Miss E. M. Brown, London (Parasitic dinoflagellates in plankton).
Dr H. H. Brown, Colonial Fisheries (Library).
A. Bulliard, Paris (General zoology).
Dr M. Burton, British Museum (Sponges).
A. T. Campbell, Penzance (General zoology).
W. T. Catton, Sheffield (Fish-blood development).
P. G. Corbin (Mackerel investigations).
E. J. Denton, London (General biology and histochemistry).
P. S. B. Digby (Planktonic Copepods).
Miss N. Duncan, Leicester (General zoology).
R. G. Evans, Aberystwyth (Intertidal ecology).
J. E. Forrest, London (Nudibranch Molluscs).
Dr V. Fretter, London (*Rissoa*).
Dr A. Graham, London (Prosobranchs).
Miss U. M. Grigg, Cambridge (Molluscs).
N. Guppy, London (Library).
R. Hamond (General zoology).
Dr J. D. F. Hardenberg, Batavia (Library).
Dr R. Harkness (Measurement of hydrogen-ion concentration).
Dr T. J. Hart, Discovery Committee (Falkland Islands' fisheries and ice diatoms).
P. H. T. Hartley, Wray Castle (Blennies).
Dr R. S. Hawes, Exeter (Gregarines of Polychaetes).
M. R. Haywood, Leicester (Mechanics of the blood vascular system in *Ascidiella*).
M. N. Hill, Cambridge (Seismic prospecting of sea-bed).
E. Hollowday (Rotifers).
N. A. Holme, Cambridge (Reproduction in Annelids and Molluscs).
G. M. Hughes, Cambridge (Neuromuscular movements in *Carcinus*).
A. Ibbotson (Library).
Dr M. W. Jepps, Glasgow (Structure of sponges).
F. G. W. Knowles, Marlborough (Colour changes in Crustaceans).
Fl.-Lieut. F. L. Litchfield (General zoology).
Miss J. Lorch, London (Bone formation in larval fish).
Dr A. G. Lowndes (Density of aquatic organisms).
Dr C. E. Lucas, Hull (Oceanography).
Miss J. Marchant, Birmingham (General zoology).
H. P. Moon, Leicester (Mechanics of the blood vascular system in *Ascidiella*).
Miss V. Moyle, Cambridge (Excretion in Amphipods).
J. A. C. Nicol, Oxford (Nervous system of Polychaetes).
Dr A. P. Orr, Millport (General).
Dr C. F. A. Pantin, Cambridge (Nerve physiology of Actinozoa).
Dr M. W. Parke (Algae).

A. Rifaat, Fouad I University, Cairo (Plankton).
J. Riley, London (Seashore Diptera).
M. J. Ritchie, London (General biology).
Dr D. M. Ross, London (General zoology).
Miss H. G. Q. Rowett, Plymouth (Library).
A. A. E. Sagay, Exeter (General zoology).
Dr P. N. Sarangdhar, Department of Fisheries, Bombay (Elasmobranchs and aquarium management).
Miss M. Sharman, Birmingham (Systematics of Lamellibranchs).
Dr J. E. Smith, Cambridge (Staining of nervous tissue of Echinoderms).
B. Sparrow (Diatoms).
Miss N. G. Sproston (Parasites of marine animals).
Miss F. A. Stanbury, Plymouth (Antifouling research).
Miss M. Sutton, London (General biology).
F. J. Taylor, Leicester (Phytoplankton and Algae).
Miss M. Taylor, Exeter (Parasites of *Phascolosoma*).
J. Theodorides, Paris (Shore entomology).
G. Thomas, Birmingham (General zoology).
A. K. Totton, British Museum (Siphonophores).
Y. R. Tripathi, Allahabad University (Parasites of fishes).
D. W. Tucker, Exeter (General zoology).
Miss Vidya Vati, Lucknow University (Fish embryology).
D. R. Wilkie, London (Measurements of hydrogen-ion concentrations).
P. T. Willmore, Cambridge (Seismic prospecting of sea-bed).
R. L. Woolley, St Andrews (Study of *Sepia* spermatophore by X-ray).

During this year of reconstruction a very large number of visitors have taken the opportunity of spending a day or two in Plymouth to see the work of the laboratory. Among these, the following have come from overseas:

Dr G. P. Baerends, Holland; Prof. K. N. Bahl, Lucknow University; Dr R. Dohrn, Naples; Dr Hermann Einarsson, Iceland; Prof. E. Fauré Frémiet, Paris; Prof. Z. Grodzinski, Cracow; Dr S. L. Hora, Bengal; Prof. J. J. Izquierdo, Mexico; Dr L. Linderstrøm-Lang and Dr H. Holter, Carlsberg Laboratory, Copenhagen; Dr A. W. H. Needler, Canada; Dr M. H. van Raalte, Leiden; Prof. S. Skowron, Cracow; Prof. R. Spärck, Copenhagen and Prof. H. C. Trumble, Australia.

Many workers from the Admiralty and other departments have also come specially for discussions with members of the Laboratory staff.

The usual Easter Vacation Courses in Marine Zoology were conducted by Mr D. P. Wilson and Mr G. A. Steven, and were attended by forty-one students from the following Universities, University Colleges and other institutions: Oxford, Cambridge, London, Aberdeen, Bristol, Leeds, Reading, Sheffield, Southampton, Cardiff, Exeter, Hull, Newcastle, Nottingham, Wray Castle and Plymouth Technical College.

Also during the Easter vacation Mr A. H. Lewis brought eight boys from Wellington College.

On 29 May 1946, the Danish research vessel *Atlantide* paid a second visit to Plymouth on her return voyage from the West African coast.

Scientific Work of the Plymouth Laboratory Staff

Physics and Chemistry of Sea-water

Dr W. R. G. Atkins, in collaboration with Dr H. H. Poole, is continuing the work with cube and other photometers, for the measurement of submarine illumination and Dr Cooper has made further determinations of the extinction coefficient using the Pulfrich photometer.

With the assistance of Dr M. A. Ellison, Dr Atkins has completed a survey of the records obtained by the photo-electric daylight recorded from 1930 to March 1941, when they ceased on account of war damage. The recorder, which was in use in the Meteorological Section of a large R.A.F. Station from 1943 to 1945, is once more installed and working at Plymouth.

The resumption of photo-electric work necessitated the restandardization of the cells and the examination of newer types as to their general suitability. With the assistance of Mr F. J. Warren a counter was incorporated in the J. H. J. Poole neon tube photometer, but its use at sea has so far been limited on account of electrical leaks. Photo-electric apparatus required for a visitor's researches upon the physiological effects of light was also provided.

During the war Dr Atkins served on the Sandbag Committee of the Ministry of Home Security. It is interesting now to record that the Danish copper naphthenate preservative, introduced to England (and subsequently manufactured here) by net-tests at Plymouth, was used on at least 22 million sandbags, and that the Olie ammoniacal copper sulphate method, also introduced by the Plymouth net-tests, was used on over 187 million bags. The bags thus treated had an average life of 2 years, at a cost for treatment of one farthing each. The grease compounded by Dr Atkins for the Admiralty before the war was adopted as the standard supply for certain largely used weapons of under-water warfare.

Investigations are much needed on the distribution of total dissolved phosphorus in the sea, because the phosphate present in the water at the beginning of each year has shown a close relation to the number of young fish caught and the general level of plankton population during the ensuing summer, throughout a period embracing 16 years' observations. With this aim Dr H. W. Harvey has been seeking a simple technique for measuring the total phosphorus present as phosphate, as dissolved organic compounds in solution, and in the microplankton, in samples of water. Hydrolysis at 140° C. has proved effective in setting free phosphate from organic compounds. Its subsequent estimation has necessitated research on the formation of molybdenum blue in order to attain sufficient precision to track down possible sources of error. This in turn has necessitated the development of a photo-electric absorption-meter. A suitable method of storing samples of sea-water for subsequent analysis has also needed investigation, in order to overcome the rapid growth of bacteria attached to, and the physical adsorption of organic phosphorus compounds on the walls of the storage vessel. Satisfactory results were obtained by 'baiting' the storage bottles with freshly precipitated aluminium hydroxide which was dissolved with acid immediately before transferring the waters to the reaction vessels.

During the early part of the year Dr Harvey completed a research on requirements for growth by species of flagellates and a *Chlorella*. At that time the inshore waters lacked sufficient manganese in solution for their continued growth. For vigorous growth the addition of about 1 mg. of this element to a ton of sea-water was necessary. The results are being published in Vol. XXVI, No. 4, of the *Journal*.

It has not been possible, owing to the lack of a research vessel during the spring, to continue the regular observations on phosphate, but Dr L. H. N. Cooper is restarting this work.

In marked contrast to the correlation between the distribution of young fish off Plymouth and the winter maximum of phosphate it has never proved possible to find any relation whatever between biological events and the hydrological environment as measured by salinity. This negative result has become so definite that it can have only one meaning—the presence of waters of similar salinity but very different hydrological and biological histories. With these two facts in mind Dr Cooper has been surveying all the physical and chemical data available in the area and trying to relate them to quantitative biological records. Correlations of inorganic phosphates have been found with the landings of herrings, spurdogs and rays and skates.

For an understanding of the distribution of salinity on the continental shelf it is essential to study the ocean waters to the west and south-west. It would appear that there are three types of high salinity water: (*a*) North Atlantic central water, with a well-defined temperature-salinity diagram, occupying the upper 600 m. well to the west and south-west, (*b*) the Mediterranean Tongue between 800 and 1200 m. with a salinity in excess of 35·5 ‰ and 67–70 % saturated with oxygen which may possibly under certain conditions be projected on to the continental shelf, and (*c*) the 'shelf blanket' formed by winter cooling of high salinity waters on the banks to the west and south-west of Ireland with a salinity usually over 35·5 ‰ and an oxygen-content over 90 % saturated. The problems are complex, so that a number of distinct but interlocking investigations have proved necessary, each of which ought to be completed before a coherent account can be published. Dr Cooper hopes to publish the results separately under the following headings:

1. The kinetic energy of the tides of the English Channel and Celtic Sea and its effect on turbulence, vertical mixing and stability of thermoclines.
2. A review of earlier work on the adjacent waters of the eastern North Atlantic.
3. A review of the hydrology of the Celtic Sea including the data collected by the mackerel investigations in 1937–39.

4. An analytic study of the dependence of water movements in the area on wind, density differences, tides and bottom configuration.

5. The contrasted hydrological distribution in the seas of the siphonophores *Muggiaea atlantica* and *M. kochi* which show much promise as biological indicators.

6. The correlation of the seasonal, annual and geographical distribution of nutrient salts with biological events, such as landings of marketable fish and distribution of plankton and bottom-dwelling invertebrates, incorporating the results of the above five papers.

Plankton

Mr F. S. Russell has resumed the observations on the abundance of young fish in relation to other plankton animals which had been made for many years before the war. Collections started in June when the research ship became available and they show that during summer, autumn and winter the conditions were very similar to those existing immediately before the war. *Sagitta setosa* was still dominant though present only in small numbers. *Muggiaea atlantica* also still predominates although for the first time a few specimens of *M. kochi* have occurred with it. Taking all things into consideration it appears fairly certain that there has been no marked recurrence of the rich *Sagitta elegans* water off Plymouth during the war.

In connexion with the researches on the biology of the mackerel population off the western entrance to the English Channel, Mr P. G. Corbin has now completed a report on the spawning of the mackerel and the distribution of the pelagic young stages. As indicated in previous reports of the Council (1938 and 1939–40), mackerel-spawning was observed in 1937–39 in the continental-shelf area from mid-March until the end of July. It starts in the west and south-west over the edge of the continental shelf, and as the season advances it shifts eastwards and slightly northwards across the area. Maximum spawning intensity occurs from mid-April until mid-May and by the end of July there is scarcely any spawning in the area, although it still continues inside the mouth of the English Channel eastwards of the line Land's End—Ushant, and also in the Irish Sea.

The 1937–39 cruises provided material for a study of the spawning of the pilchard and the distributions of the two *Sagitta* species which occur at Plymouth—*S. elegans* and *S. setosa*, and of the more oceanic *S. serratodentata* and *S. lyra*, and also of the siphonophore *Muggiaea atlantica*.

Large catches of pilchard eggs were taken from April to July at the western end of the Channel, in the area Land's End—Start Point—Cap de la Hague—Ushant. This region appeared to be the main spawning centre of the species although eggs were found well to the westward of the Scillies.

From the above remarks, it is clear that in April the spawning areas of the mackerel and pilchard are separate. By July, however, there is almost complete overlapping, brought about by the eastward shift of the mackerel-spawning area.

In the continental-shelf area, *Sagitta elegans* appeared to be the dominant *Sagitta* species, while *S. setosa* dominated the restricted regions of the Bristol Channel mouth and the English Channel mouth. *S. serratodentata*, although occurring within the continental-shelf area, was dominant only along the edge, above the 100 fathom line. *S. lyra* was entirely restricted to the edge of the continental shelf and was never dominant.

Muggiaea atlantica occurred mainly in the mouth of the English Channel and was seldom taken far to the west of the Scillies except in June 1939. Its distribution in April 1937 and 1939 appeared to show a correlation both in extent and numbers with an inflow into the Channel mouth of low salinity water ($<35{\cdot}10\ ^0/_{00}$) from the Ushant area. In April 1938 when there was scarcely any inflow of fresh water into the southern half of the Channel mouth, it was entirely absent from this region.

A paper on the distribution of the pelagic young stages of teleosteans other than the mackerel is in course of preparation, and it is hoped that the plankton collections will yield sufficient material to enable the life-cycle of *Sagitta serratodentata* to be worked out.

Fauna of the Sea-floor

Mr D. P. Wilson has made further observations on polychaetes and has been successful in rearing for the first time a member of the family Opheliidae, *Ophelia bicornis* Sav. which has a pelagic development lasting normally about two weeks. The early larva is a small trochosphere with a large apical tuft, a broad prototroch and a small telotroch. At metamorphosis it has three bristle segments and is provided with a number of papillae which enable it to cling firmly to solid objects such as sand grains. This seems to be an adaptation to settlement on sand banks swept by swift tidal currents, as are those of Exmouth where the species is plentiful. The adult lives in very clean moderately coarse sand and striking results were obtained when larvae ready to metamorphose were tested with a variety of bottom deposits, natural and artificial. Briefly it can be stated that when given sand from the normal adult habitat larvae metamorphose readily, but much less readily, or not at all, when kept in vessels containing deposits of a different character. They retain the ability to metamorphose for several weeks. Further experiments to determine as far as possible the nature of the stimulus initiating metamorphosis will be undertaken during the next breeding season.

Mr Wilson published, in the *Journal*, Vol. XXVI, No. 3, an account of the capture of prey by *Sepia officinalis* L. This was illustrated by photographs revealing a number of points not previously recorded. The paper gives a fuller account of the hunting methods of this cuttlefish than has previously been available in the literature. Mr Wilson's observations on the triradiate and other forms of *Nitzschia closterium* (Ehr.) W.Sm. forma *minutissima* Allen and Nelson also appeared in the same number of the *Journal.*

During the year the National Oil Refineries Ltd., Neath, asked the Association for advice on methods of combating the ravages of *Teredo*, which had appeared in abundance towards the end of the war in the piles of the jetties and breasting blocks in their Queen's Dock at Swansea. Mr Wilson and Mr Steven, in January 1946, went to Neath to make an inspection on the spot. A full report was made to the Company who were advised to try the effect of detonating small explosive charges under water close to the piles. This was done and samples of blasted and unblasted timber sent to Plymouth showed clearly a very high death-rate among *Teredo* near the explosions, with no damage to the wood. Blasting was, therefore, carried out on an extensive scale and further samples have shown that the majority of the *Teredo* have been killed throughout the dock. It is evident, however, from examination of test-blocks that a source of infection still exists and further blasting to kill the young *Teredo* has been advised. Results obtained give reason to hope that *Teredo* attack can be kept at negligible intensity by regular and adequate blasting.

Mr G. M. Spooner has written up part of his studies on the distribution of *Gammarus* species in British estuaries, which will appear in Vol. XXVII, No. 1, of the *Journal.* This contribution deals mainly with the taxonomy of the species. Apart from attempting to fill existing gaps in detailed description of adult males, it was necessary to establish reliable means of identifying the females and immatures from mixed samples. This has been successfully accomplished. The useful, and unexpected, discovery (reported before the war) that the variable *G. zaddachi* can be separated into two distinct morphological forms, with different salinity optima, has necessitated some detailed additions to existing descriptions of this species. The two forms are separated as subspecies: *G. z. zaddachi* the more hairy form (embracing the 'freshwater' and 'intermediate' forms of Sexton) is retained as the typical subspecies, from which *G. z. salinus* ('brackish water' form of Sexton) is separated. The variation due to environmental influences must at least be more limited than has previously been supposed. However, within *G. z. zaddachi* itself there is appreciable variation in the density and length of hairs, and it is still possible that populations breeding in pure fresh water (e.g. River Elbe and North Ireland) may prove to belong to a distinct race: though they cannot be absolutely separated from the hairiest of animals living at the heads of estuaries.

The next contribution will deal with the population samples from different estuaries. The changes in the *Gammarus* population follow closely the salinity gradient, oscillating with it between winter and summer conditions, and (where the tidal zone is broad) showing comparable differences between the upper part of the tidal zone and low water. The *Gammarus* population can therefore serve as a 'biological indicator' for salinity conditions.

Another aspect of the work involves experimental observations on living *Gammarus zaddachi* in the laboratory. As reported before the war, preliminary observations had indicated that the 'brackish water form' of *G. zaddachi*, now named subspecies *salinus*, was incapable of breeding with the typical 'hairy' form of the species. A detailed experiment to verify this important conclusion was carried out this year, and the summer months were devoted to this experiment almost exclusively. The results confirm completely that the two forms are sterile to one another, whichever way the cross is made. The eggs may pass through the early stages of segmentation, but they never produce embryos. An equal number of control matings were made concurrently, and the animals were given turns in crosses and controls. At the same time further evidence has been obtained that the similar forms from different estuaries are normally fertile with one another.

Further experiments in hand are designated to test other preliminary observations which have shown that the two subspecies retain their diagnostic characters whatever the salinity of the water in which they are reared.

To supplement the morphological work on British species, a useful collection of samples from northern Europe, kindly lent by the late Dr K. Stephensen of Copenhagen, has been examined.

Mrs E. W. Sexton has continued her work on the Amphipod species *Jassa falcata* (Mont.). She has traced its history from its establishment in 1808, through its many changes of name, generic as well as specific, which have caused so much confusion. The diverse developmental forms, described by different observers as new species, have been shown to be only the growth stages of the one species. It is a littoral or sub-littoral species, with a wider distribution than any other amphipod yet known to science. Its records, ranging from the coasts of Norway to the Antarctic, have been investigated, and are given with the names of the authors responsible for them.

Mr H. G. Vevers has started investigations on some aspects of the breeding biology of the Plymouth echinoderms. It is already well known that after the breeding season echinoderm gonads in general undergo a marked atrophy accompanied by phagocytosis, and a detailed study is now being made of the histological changes occurring in the gonads of a number of echinoderms at different times of the year. The present investigation and later experiments are designed to throw some light on the factors controlling the various phases of the breeding cycle in this group. The relationship between temperature and the breeding cycle is still by no means clear. More attention should be paid to other factors, e.g. chemical or nutritional, which may enter into the problem. Concurrently with this work data are also being collected on the sex ratio of populations of echinoderms, and here again the observations collected at different times of the year are being recorded separately, as there is evidence from the work of a French author that, in at least one species (an Echinoid), the sex ratio varies according to season.

A review is being prepared of existing knowledge on sexual dimorphism in echinoderms (apart from that associated with brood protection), and observations are being made on a number of species to determine whether sexually dimorphic characters exist. Such characters are already known and easily demonstrable in *Psammechinus miliaris* and *Echinocyamus pusillus*, and in view of the many uses to which the genital products of echinoderms are put in experimental work it is desirable that satisfactory methods should be found of sexing the individuals of as many echinoderm species as possible, without killing the animals. A fairly satisfactory method has already been found of sexing ripe *Ophiothrix fragilis* without permanent injury to the animals themselves.

Preliminary work is also being done on a method of administering natural and synthetic sex hormones to Crustaceans, with a view to tracing the effect of these substances on the morphogenesis of sexually dimorphic characters in this group.

Physiology of Marine Animals

Dr J. F. Danielli, who left the staff in October 1946, has been developing new methods for cytochemistry, particularly for the cytological localization of tryptophane, phenols, histidine and nucleic acid. These methods have been used in the study of chromosome structure. They show that the greater part of the nucleic acid, histidine, tryptophane and tyrosine of chromosomes is concentrated in the chromomeres. Under his direction Miss J. Lorch has been studying mechanisms of bone formation in fishes.

Fishes and Fisheries

Supplementary to his work on vertebral variation in teleostean fishes, Mr E. Ford has been studying the variation in the form of the neurocranium in gadoid species. The gadoid fishes were chosen because a good representative collection of skulls, prepared before the war, had escaped damage when the laboratory was wrecked by bombing. Mere cursory comparison between the skulls of the different species showed that they had much in common, and it was thought that it would be instructive to determine whether, by following the method of transformations suggested by D'Arcy Thompson in *Growth and Form*, one could arrive at some one basic gadoid form of neurocranium. There arose, however, the practical difficulty of finding a method of orientating in space such a complex figure as the outline of a fish's skull. The one eventually adopted was to mark dots in indian ink at what appeared to be the natural centres of symmetry for each of the individual bones of the neurocranium, as indicated by the radial striations and concentric growth rings. Having done so, the dots were seen to be disposed in an orderly, geometric network. Investigation of the geometry of this network in the cod most strongly indicated that it conformed very well to an hexagonal system of symmetry. This indication has been followed up, with interesting results, on the hypothesis that the skulls of other gadoid species conform to the same system of symmetry as seen in the cod.

Mr G. A. Steven has been writing up the results of Mackerel Researches carried out from this laboratory before the outbreak of the war. Extremely interesting and important information on the migrations of this fish are emerging from the work. It has been found that mackerel of the English Channel, Irish Sea and Celtic Sea areas have only one main spawning ground in the open sea about 100 miles west of the Scilly Islands. After spawning they disperse all along the shores until late autumn when they concentrate in restricted and localized positions on the sea-floor. These concentrations take place in the close vicinity of well-defined irregularities in the level of the sea-bottom—e.g. acclivities caused by raised banks such as the Vergoyer at the entrance to the Dover Straits, and declivities provided by sharp depressions such as the Hurd Deep, in the English Channel—and are independent of depth. Some fish therefore remain at suitable places in the English Channel, others near the Smalls and Saltees on either side of St George's Channel. Still more seek bottom around the many banks and deeps in the Celtic Sea, and many—perhaps the great majority—concentrate along the edge of the continental slope itself. In spring they all rise and become pelagic again and migrate to the spawning ground. Thus fish converge on this ground from all directions in the spring; and there is not a simple anadromous migration from deep to shallow water to spawn as has previously been thought.

Data on age, growth-rate, and spawning habits are also being worked up.

In the course of the year two Reports, originally submitted to the Sierra Leone Government during the war, have been partly rewritten for publication by the Crown agents for the Colonies.

Research on Parasites

During the year Miss N. G. Sproston has continued her researches on marine parasites. *Ichthyosporidium hoferi*, the fungoid organism causing disease in mackerel and pilchard, has received further study regarding its effects on the fish. A decline in the mackerel fishery has restricted samples from all sources this year; but some mackerel have been obtained from time to time from the Torry Research Station, Aberdeen, and a visit was made to Newlyn where a large sample of fresh pilchard was examined. The results from the Scottish mackerel agreed with those from locally caught fish in showing a remission in both the intensity and the incidence of this pathogenic infection as the season advanced; this is the first time a sustained and generalized remission in the endemic has been found since the disease was first noted in mackerel at Plymouth in 1940. The similar disease in pilchard showed a comparable remission, though the percentage of infection was not reduced so markedly as in the mackerel.

During the examination of these fishes the usual metrical data have been collected, partly for analysis of the factors correlated with the disease, and partly for the use of Mr G. A. Steven in his long-term investigations on the mackerel stock. The data thus accumulated since 1940 have been treated statistically by Mr G. M. Spooner who has confirmed the results of the preliminary graphical analyses, that there is no significant change in the condition factor of the mackerel associated with the severity of the disease: a fact difficult to explain in view of the extensive necrosis of the vital organs when the infection is active. In addition, there have emerged from Mr Spooner's statistical analysis certain other facts associated with the condition factor of this fish, which it is thought will have significance in the study of other species.

Investigations on the parasitic fauna of fishes have been continued, and include the examination of some rare visitors to these coasts. Some sea-birds have also been examined, with a view to tracing the adults of larval parasites occurring in fishes. During the year some sixty species of Helminth and Crustacean parasites have been found which require reinvestigation, and some of these will undoubtedly prove to be new to science. A study is now in progress on the phyllobothriid cestodes of selachians—up till now rather poorly represented in our fauna, but recent dissections have provided a wealth of material.

The long work on the monogenetic trematodes has now been published in the *Transactions of the Zoological Society of London*.

Miss Sproston left Plymouth at the beginning of March 1947, to take up an appointment as Research Fellow in the Academia Sinica, Shanghai.

Research on Algae

Although the mass of data collected by Dr M. W. Parke has not yet been fully worked up, many interesting facts have already emerged. The study of *Laminaria saccharina* has been completed. This is the shortest lived of perennial British Laminariaceae, reaching its peak of growth during the second year and not surviving much beyond three years.

There is evidence that the gametophyte generation can be fertile throughout the year and may itself under certain conditions be perennial. The sporophyte generations can be initiated at any time of year, but under certain circumstances—e.g. in the exposed littoral zone—they may not persist to maturity, nor do winter-developed sporophytes occur in the sublittoral zone. The bulk of the population found on the shore at any time of year consists of spring-developed plants.

Although the sporophyte shows continuous growth throughout life there are alternating periods of rapid and slow growth. Growth is most rapid from January to July gradually increasing until March, remaining at a maximum until May or June and gradually slowing down to a minimum during the period September to December. Rate of growth also shows variations according to age and habitat.

These changes in rate of growth are shown as light and dark rings in sections of the perennial stipe and holdfast, the darker rings representing the slow growth. These rings form a valuable index of the age and growth of a plant.

The development of the new series of haptera in the holdfasts takes place during the period of rapid growth, although the beginning of new meristematic tissue above the old haptera can sometimes be detected as early as November. The detachment of plants during their third year is probably because new haptera are rarely formed in that year of growth.

The fruiting of the sporophyte appears to depend on the age of the tissue surviving on the distal part of the frond, which must be at least 6 months old. The age of the distal frond tissue appears to be controlled by the time of initiation of the plant and the nature of its habitat.

In British waters *L. saccharina* plants can become mature when eight to nine months old, and fruiting plants can be found at all times of year with a maximum from October to February.

The Library

The thanks of the Association are again due to numerous foreign Government Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the *Journal*. Thanks are also due to those who have sent books or reprints of their papers, which are much appreciated.

Published Memoirs

Vol. XXVI, No. 3, of the *Journal* of the Association was published in July 1946, and Vol. XXVI, No. 4, is nearing completion.

The following papers, the outcome of work done at the laboratory, have been published elsewhere than in the *Journal* of the Association:

Atkins, W. R. G., 1945. Daylight and its penetration into the sea. *Trans. Illuminating Eng. Soc.* (London), Vol. X, No. 7, pp. 1–12.

Fox, D. L. & Pantin, C. F. A., 1941. The colours of the plumose anemone *Metridium senile* (L.). *Phil. Trans. Roy. Soc.* Ser. B, Vol. CCXXX, pp. 415–50.

Fox, D. L. & Pantin, C. F. A., 1944. Pigments in the Coelenterata. *Biol. Rev.* Vol. XIX, pp. 121–34.

Fretter, Vera, 1946. The pedal sucker and anal gland of some British Stenoglossa. *Proc. Malacol. Soc.*, Vol. XXVII, pp. 126–30.

Hall, D. M. & Pantin, C. F. A., 1937. The nerve-net in the Actinozoa. V. Temperature and facilitation in *Metridium senile*. *Journ. Exp. Biol.*, Vol. XIV, pp. 71–8.

Harvey, H. W., 1946. *Fertility of the Ocean.* Discussion on Oceanography, Linnean Society of London, 1946, pp. 5–8.

Hodgkin, A. L. & Huxley, A. F., 1946. Potassium leakage from an active nerve-fibre. *Nature*, Vol. CLVIII, pp. 376–7.

Lebour, M. V., 1946. The Oyster, I. *School Science Review*, Vol. XXVIII, pp. 81–6.

LISSMANN, H. W., 1946. The neurological basis of the locomotory rhythm in the spinal dogfish (*Scyllium canicula, Acanthias vulgaris*). I. Reflex behaviour. *Journ. Exp. Biol.*, Vol. XXIII, pp. 143–61.

LISSMANN, H. W., 1946. The neurological basis of the locomotory rhythm in the spinal dogfish (*Scyllium canicula, Acanthias vulgaris*). II. The effect of de-afferentation. *Journ. Exp. Biol.*, Vol. XXIII, pp. 162–76.

LOWNDES, A. G., 1947. Recent work on flagellar movement. *Science Progress*, Vol. XXXV, pp. 62–8.

MOORE, J. GRANGE, 1947. The determination of the depths and extinction coefficients of shallow water by air photography using colour filters. *Phil. Trans. Roy. Soc.*, Ser. A, Vol. CCXL, pp. 163–217.

ROSS, D. M. & PANTIN, C. F. A., 1940. Factors influencing facilitation in Actinozoa. The action of certain ions. *Journ. Exp. Biol.*, Vol. XVII, pp. 61–73.

RUSSELL, F. S., 1946. What is Biology? *School Science Review*, Vol. XXVIII, pp. 69–79.

RUSSELL, F. S., 1946. *Marine Zoology*. Discussion on Oceanography, Linnean Society of London, 1946, pp. 8–10.

SANDERS, F. K. & YOUNG, J. Z., 1940. Learning and other functions of the higher nervous centres of *Sepia*. *Journ. Neurophys.*, Vol. III, pp. 501–26.

SMITH, J. E., 1946. The mechanics and innervation of the starfish tube foot-ampulla system. *Phil. Trans. Roy. Soc.*, Ser. B, Vol. CCXXXII, pp. 279–310.

SPROSTON, NORA G., 1946. A synopsis of the monogenetic Trematodes. *Trans. Zool. Soc.*, London, Vol. XXV, pp. 185–600.

THOMAS, H. J., 1944. Tegumental glands in the Cirripedia Thoracica. *Quart. Journ. Micro. Sci.*, Vol. LXXXIV, pp. 257–82.

WILSON, D. P., 1946. The seashore life of the British Isles. *Geographical Magazine*, Vol. XIX, pp. 264–71.

Membership of the Association

The total number of annual members on 31 March 1947 was 351, being 27 more than on 31 March 1946. The number of life members was 61. The number of associate members is now four, Sir Joseph Barcroft, F.R.S., having died during the year.

Finance

General Fund. The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

Private Income. The Council gratefully acknowledge the following generous grants and donations for the year:

From the Fishmongers' Company (£500), the Royal Society (£50), British Association (£50), Physiological Society (£30), Magdalen College, Oxford (£25), and the Cornwall Sea Fisheries Committee (£10). The following sums have also been received as rentals of tables in the laboratory: the Universities of Cambridge (£105), London (£105), Oxford (£52. 10*s.*), Bristol (£25), Birmingham (£15. 15*s.*), Manchester (£10. 10*s.*), Leeds (£20), Nottingham (£10. 10*s.*), Leicester (£10. 10*s.*), Exeter (£10. 10*s.*), Sheffield (£5), the Ray Lankester Fund (£20) and the Imperial College of Science and Technology (£10).

President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1947–48:

President

Prof. James Gray, C.B.E., M.C., Sc.D., LL.D., F.R.S.

Vice-Presidents

The Earl of Stradbroke, K.C.M.G., C.B., C.V.O.
The Earl of Iveagh, C.B., C.M.G.
Viscount Astor
Sir Nicholas Waterhouse, K.B.E.
Sir Sidney Harmer, K.B.E., Sc.D., F.R.S.
Col. Sir Edward T. Peel, K.B.E., D.S.O., M.C.
The Rt. Hon. Sir Reginald Dorman-Smith
Prof. Walter Garstang, D.Sc.
The Rt. Hon. Tom Williams, M.P.

COUNCIL

To retire in 1948

Prof. C. M. Yonge, D.Sc., F.R.S.
Admiral Sir John Edgell, K.B.E., C.B., F.R.S.
Prof. J. H. Orton, D.Sc.
E. Baldwin, Ph.D.
G. P. Wells

To retire in 1949

G. E. R. Deacon, D.Sc., F.R.S.
Prof. J. E. Harris, Ph.D.
N. A. Mackintosh, D.Sc.
Edward Hindle, Sc.D., F.R.S.
R. S. Wimpenny

To retire in 1950

H. Cary Gilson
C. F. Hickling
Morley H. Neale
Prof. Lily Newton, Ph.D.
Prof. J. Z. Young, F.R.S.

Hon. Treasurer

Major E. G. Christie-Miller, 38 Hyde Park Street, London, W. 2

Secretary

F. S. Russell, D.S.C., D.F.C., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. Bidder, Sc.D.
P. D. H. Dunn, C.M.G., O.B.E. (Ministry of Agriculture and Fisheries)
The Worshipful Company of Fishmongers:
  The Prime Warden
  Major E. G. Christie-Miller
Prof. A. C. Hardy, D.Sc., F.R.S. (Oxford University)
C. F. A. Pantin, Sc.D., F.R.S. (Cambridge University)
Prof. H. Gordon Jackson, D.Sc. (British Association)
H. G. Maurice, C.B. (Zoological Society)
Prof. A. V. Hill, C.H., O.B.E., Sc.D., F.R.S. (Royal Society)

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH 1947

	£	s.	d.	£	s.	d.	£	s.	d.
SUNDRY CREDITORS:									
Accrued Expenses				409	17	11			
Subscriptions received in advance				31	9	0			
Grant received in advance				125	0	0			
Admiralty—Hire of R.V. 'Sabella'				1150	0	0	1716	6	11
BANK OVERDRAFT							—	—	—
AQUARIUM GUIDE PRINTING FUND:									
As at 31st March 1946				22	8	6			
Add: Sale of Aquarium Guides ...	14	12	4						
Sale of Postcards	7	6	0	21	18	4			
Transfer to Aquarium Sinking Fund ...				10	17	1			
				55	3	11			
Less: Purchases									
Guides	22	8	7						
Postcards	32	15	4	55	3	11	—	—	—
AQUARIUM SINKING FUND:									
Transfer from Income and Expenditure Account				343	1	0			
Less: Transfer from Aquarium Guide Printing Fund				10	17	1	332	3	11
SPECIAL APPARATUS FUND:									
As at 31st March 1946				10	4	11			
Less: Expenditure				10	4	11	—	—	—
E. T. BROWNE—BEQUESTS FUNDS:									
Building Fund, as at 31st March 1946	1227	16	5						
Interest on Investment	37	5	4	1265	1	9			
Library Fund, as at 31st March 1946	1085	0	8						
Interest on Investment	33	1	5	1118	2	1			
Special Apparatus Fund, as at 31st March 1946	2466	1	5						
Interest on Investment	74	15	11	2540	17	4			
Scientific Publications Fund, as at 31st March 1946	1849	10	10						
Interest on Investment	56	1	10	1905	12	8	6829	13	10
'SALPA' DEPRECIATION FUND:									
As at 31st March 1946				5899	15	8			
Add: Amount receivable from Ministry of Transport on account of Hire				402	0	0			
Interest on Investments				175	8	0	6477	3	8

	£	s.	d.	£	s.	d.	£	s.	d.
BOATS AND EQUIPMENT, at valuation as estimated by the Director at 31st March 1941 plus Additions at Cost:									
S/S 'Salpa'				2000	0	0			
Motor Boat 'Gammarus':									
As at 31st March 1946	150	0	0						
Additions during the year ...	50	0	0	200	0	0			
Nets, Gear and General Equipment:									
As at 31st March 1946				50	0	0	2250	0	0
LABORATORY APPARATUS, ENGINES AND PUMPS, at valuation as estimated by the Director at 31st March 1941, plus additions at cost:									
As at 31st March 1946				4300	0	0			
Additions during the year				500	0	0	4800	0	0
LIBRARY, at valuation by Mr Ridgill Trout in January 1941 plus additions at cost:									
As at 31st March 1946				16070	0	0			
Additions during the year				30	0	0	16100	0	0
STOCKS ON HAND, as valued by the Director:									
Specimens				600	0	0			
Chemicals				250	0	0			
Journals				400	0	0	1250	0	0
SUNDRY DEBTORS:									
Sales of Specimens, etc.				333	3	0			
Ministry of Transport—Hire of S/S 'Salpa' ...				33	10	0			
Ministry of Agriculture and Fisheries—Fourth instalment of Grant from Development Fund for 1945–6				—	—	—	366	13	0
PREPAYMENTS							174	13	0
RECOVERABLE EXPENDITURE:									
Research Fund—Miss N. G. Sproston:									
Expenditure				436	13	9			
Less: Grant received	262	10	0						
Balance at 31st March 1946...	8	5	11	270	15	11	165	17	10
GENERAL FUND INVESTMENT, at market value as at 31st March 1931 of £352. 2*s.* 3*d.* 3% Local Loans, converted during the year to £352. 2*s.* 3*d.* 2½% Treasury Stock							232	7	10
(Market value at date £338. 0*s.* 7*d.*)									
E. T. BROWNE—BEQUESTS FUNDS INVESTMENT, at cost:									
£6905. 3*s.* 6*d.* Conversion Loan 3%							6829	13	10
(Market value at date £7008. 15*s.* 0*d.*)									
'SALPA' DEPRECIATION FUND INVESTMENTS, at cost:									
£590. 6*s.* 0*d.* 2½% Treasury Stock				506	10	9			
£5823. 16*s.* 2*d.* Conversion Loan 3%				5937	2	11			
(Market value at date £6477. 16*s.* 9*d.*)							6443	13	8

	£ s. d.	£ s. d.	£ s. d.
REPAIRS AND RENOVATIONS FUND:			
As at 31st March 1946		501 17 6	
Add: Transfer from Income and Expenditure Account		50 0 0	
Interest on Investment		12 17 10	
		564 15 4	
Less: Transferred to 'Gammarus' Replacement Fund		564 15 4	— — —
'GAMMARUS' REPLACEMENT FUND:			
Transfer from Repairs and Renovations Fund ...			564 15 4
COMPOSITION FEES FUND:			
As at 31st March 1946		362 5 0	
Add: Fees Received		110 5 0	472 10 0
RESEARCH FUND—P. S. B. DIGBY:			
Grant received		229 0 0	
Less: Expenditure		221 6 2	7 13 10
BIOLOGICAL INVESTIGATIONS ON ALGAE FUND:			
Grant received		713 13 11	
Less: Balance at 31st March 1946...	71 18 11		
Expenditure	633 13 9		
		705 12 8	8 1 3
MACKEREL RESEARCH FUND:			
Grant received		425 0 0	
Less: Expenditure		415 4 1	9 15 11
BUILDINGS RECONSTRUCTION FUND:			
Received during the year		1042 19 8	
Add: Transfer from Surplus Account		1879 3 9	
		2922 3 5	
Less: Balance due at 31st March 1946...	1400 0 0		
Expenditure	150 0 0		
		1550 0 0	1372 3 5
CAPITAL RESERVE ACCOUNT:			
As at 31st March 1946			21688 8 2
SURPLUS ACCOUNT:			
As at 31st March 1946		4497 19 1	
Add: Excess of Income over Expenditure for the year...		801 3 7	
		5299 2 8	
Less: Transfer to Buildings Reconstruction Fund		1879 3 9	3419 18 11
			£42,898 15 2

JOHN E. HARRIS
O. D. HUNT } *Members of the Council.*

	£ s. d.	£ s. d.
'GAMMARUS' REPLACEMENT FUND INVESTMENT, at cost:		
£553. 8*s.* 6*d.* Conversion Loan 3%		564 15 4
(Market value at date £561. 14*s.* 6*d.*)		
COMPOSITION FEES FUND INVESTMENTS, at cost:		
£18. 8*s.* 6*d.* 2½% Treasury Stock...	15 15 0	
£447. 8*s.* 2*d.* Conversion Loan 3%	456 15 0	
(Market value at date £471. 16*s.* 2*d.*		472 10 0
CASH AT BANK AND IN HAND:		
Coutts and Company	2650 3 6	
Lloyds Bank Limited	547 11 5	
Cash in Hand	50 15 9	3248 10 8
		£42,898 15 2

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the Books of the Association and have obtained all the information and explanations we have required. Capital Expenditure on erection of Buildings on Land held on Lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs as at 31st March 1947 according to the best of our information and the explanations given to us and as shown by the books of the Association.

PRICE, WATERHOUSE & CO.
Prudential Buildings, George Street, Plymouth.
15*th May*, 1947.

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1947

	£	s.	d.	£	s.	d.
To Salaries, including Association's Contributions to Superannuation and War Bonuses ...				10308	17	5
,, Laboratory and Boats' Crews' Wages, including National Insurance, Contributions to Superannuation Scheme, War Bonuses and Employers' Liability Insurance ...				8243	1	2
,, Upkeep of Library				366	14	3
,, Scientific Publications, less Sales				612	11	0
,, Upkeep of Laboratories and Aquarium, etc.:						
Buildings and Machinery	859	5	0			
Electricity, Oil, Gas, Coal and Water ...	499	4	1			
Chemicals and Apparatus	940	18	7			
Fire Insurance, Tithe, Ground Rent and Rent of Store	86	3	11			
Travelling Expenses	313	14	3			
Stationery, Postages, Telephone, Carriage and Sundries	624	11	3			
Specimens	187	15	1			
Architect's Fee for Plans for Reconstruction of Buildings	—	—	—			
				3511	12	2
,, Expenditure in Connection with R.V. 'Sabella'				674	9	8
,, Maintenance and Hire of Boats:						
Petrol, Oil, Paraffin, etc.	173	19	7			
Maintenance and Repairs with Nets, Gear and Apparatus	373	3	6			
Purchase of Materials for Nets, etc. for Sale	349	7	5			
Boat Hire and Collecting Expenses	53	14	5			
Insurances	331	11	0			
Hire of R.V. 'Sabella'	1150	0	0			
				2431	15	11
,, Bank Charges				34	12	2
,, Transfer to Repairs and Renovations Fund				50	0	0
,, Transfer to Buildings Reconstruction Fund				—	—	—
,, Transfer to Aquarium Sinking Fund ...				343	1	0
,, Balance, being Excess of Income over Expenditure for the year				801	3	7
				£27,377	18	4

	£	s.	d.	£	s.	d.
By Grants:						
Ministry of Agriculture and Fisheries Grant from Development Fund	23111	12	0			
Fishmongers' Company	500	0	0			
British Association	50	0	0			
Royal Society	50	0	0			
Physiological Society	30	0	0			
Cornwall Sea Fisheries Committee	10	0	0			
				23751	12	0
,, Subscriptions (excluding Subscriptions received in advance)				353	16	7
,, Donations...				26	16	0
,, Fees for Tests of Materials (*less* £60 for Raft)				137	8	0
,, Sales:						
Specimens	1432	9	7			
Photographs (*less* purchases)	95	5	5			
Fish	125	11	5			
Nets, Gear and Hydrographical Apparatus ...	276	19	11			
				1930	6	4
,, Table Rents (including University of Cambridge £105; London £105; Oxford £52. 10*s*. 0*d*.; Bristol £25; Leeds £20; Birmingham £15. 15*s*. 0*d*.; Manchester £10. 10*s*. 0*d*.; Leicester £10. 10*s*. 0*d*.; Nottingham £10. 10*s*. 0*d*.; Exeter £10. 10*s*. 0*d*.; Sheffield £5; Imperial College £10; Trustees of Ray Lankester Fund £20 and Ministry of Works £104)				800	17	7
,, Aquarium Receipts:						
Admission Fees	342	0	0			
Donation	1	1	0			
				343	1	0
,, Interest on Investments				21	5	10
,, Sale of Dr M. V. Lebour's Book				4	17	6
,, Sale of 'Plymouth Marine Fauna'				7	17	6
,, Balance of Expenditure on War Damage Repairs written off in earlier years recovered from War Damage Commission				—	—	—
				£27,377	18	4

THE GERMAN HYDROGRAPHIC JOURNAL

The Inter-allied Board of Directors of the German Hydrographic Institute, now functioning in Hamburg, propose soon to start the publication of a new journal, to be known as the *German Hydrographic Journal*. It will appear under the supervision of Dr G. Boehnecke, who is the German Director of the Institute, and will be edited by Dr Arnold Schumacher.

The *German Hydrographic Journal* will be the medium for the publication of articles on those branches of science which are the concern of the German Hydrographic Institute. These are: coastal and open sea surveying, nautical science, navigation, chronometry, terrestrial magnetism, ship's magnetism, nautical technics, tides, and physical and chemical oceanography—the latter inclusive of reports on sea-bottom geology and lithology. The journal will, in effect, so far as the subjects named are concerned, take the place of the former *Annalen der Hydrographie und Maritimen Meteorologie* which were published by the German Admiralty from 1873 to 1891, and thereafter by the Deutsche Seewarte up to 1944.

Maritime meteorology and climatology, being now the concern of the Meteorological Office for North-Western Germany, will receive attention in the new journal only in oceanographical connexions.

As far as possible, each issue will contain articles on a variety of the subjects named above, and will include also notices on hydrographic institutions and other related matters.

In addition, notices and/or reviews of publications of interest to the Institute will appear in the pages of the journal, together with a current bibliography relating to the special fields of research enumerated.

An ultimate aim is gradually to list all German and other publications of relevance which have appeared since autumn 1939, though such a bibliography cannot be compiled in proper time sequence.

THE DISTRIBUTION OF IRON IN THE WATERS OF THE WESTERN ENGLISH CHANNEL

By L. H. N. Cooper, D.Sc., F.R.I.C.
Chemist at the Plymouth Laboratory

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(Text-figs. 1–2)

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Introduction

Iron is essential for all plants and animals, but only a small supply is available in sea water. Since most compounds of iron are very sparingly soluble in neutral or alkaline solution, their distribution in the sea may follow a very different pattern from that of phosphate and nitrate. Earlier it had been shown (Cooper, 1935; Thompson & Bremner, 1935*b*; Rakestraw, Mahncke & Beach, 1936) that the distribution of iron in the sea was very erratic, even under conditions when vertical mixing would be expected to be thorough, so that much of it must be particulate and subject to random distribution (cf. Harvey, 1945, pp. 34, 136). The fluctuations in the iron content of small replicate samples of sea water may be large, so that either very large volumes of water must be examined, as in net methods for capturing plankton, or chemical analyses on small volumes of water must be submitted to statistical scrutiny. The precision of the analytical method has consequently been first assessed before proceeding to examine samples of water collected in the western

English Channel at the time of the midwinter maximum of dissolved inorganic phosphate. This approach has yielded considerable information as to the nature and distribution of iron in the sea and of the size and numbers of particles containing iron. Evidence has also accrued for the concentration of iron in the surface film and in the layers of water next the bottom. In certain restricted areas the bottom concentration of iron appears to be removed by suspension feeding animals. On occasion particulate ferric phosphate was present.

STATISTICAL DESIGN

The known random distribution of iron demanded statistical methods which were unnecessary for the parallel examination of phosphate and silicate. For total iron (and similarly for reducible iron) the plan had been to analyse three sub-samples at each depth worked at a limited number of stations, but two events interfered with this. First, the occurrence of several 'untrustworthy' phosphate results (see p. 298) caused samples meant for iron analyses to be used for replicate phosphates. Secondly, other samples brought in for duplicate phosphates were actually analysed singly for iron: more information, especially about ferric phosphate, was thus obtained at the expense of the symmetry of the experiment.

Throughout this paper, to have convenient units for the analyses of variance, results are reported as mg.-atom/m.^{3} × 100, that is the unit of measurement is 1 in 10^{11}. This, for brevity, will henceforth be called a 'unit'. Table I will enable the reader mentally to convert results to his own favoured units. For computation the atomic weight of iron should however be taken as 55·84.

TABLE I

Each vertical column represents a given quantity of iron in different units

mg.-atom/m.^{3} × 100 Fe	100	1	1·8	1·25
mg.-atom/m.^{3} Fe μg.-atom/l. Fe	1	0·01	0·018	0·0125
mg./m.^{3} Fe μg./l. Fe	56	0·56	1	0·7
mg./m.^{3} Fe_2O_3 μg./l. Fe_2O_3	80	0·80	1·4	1

Although, to comply with conventional chemical usage, statistical means and standard deviations are reported to no more significant figures than would be given for single analyses, all calculations have been made to four or five places by machine.

ANALYTICAL METHODS

In 1936 the reagent, 2:2′-dipyridyl, was used exactly as before (Cooper, 1935, pp. 420–24). In 1946–47 a number of small but important alterations were made.

Reducible iron. Into a 250 ml. flask 150 ml. of sea water from a very well-shaken sample bottle were introduced and treated with 0·30 ml. 4 N-HCl and

1·5 ml. of freshly prepared 10% sodium sulphite to give a solution having a pH around 2·8. After at least 4 and preferably 18 hr. 0·4 ml. 4 N-ammonium acetate and 1·5 ml. 0·4% dipyridyl in 0·2 N-HCl were added to give a pH around 5·0. After a further 4 hr. the depth of colour of the sample in a 25 cm. absorption tube was determined with the Pulfrich photometer using the blue-green S50 spectral filter.

As a result of Buch's (1942) careful examination of the method further modifications may be needed but at the time of the cruise a translation of his Swedish text was not available. This paper will be considered at a later date in connexion with the chemistry of ferrous-*tris*-dipyridyl.

Total iron sensu strictu. Strictly total iron can be determined only if the water and everything in it is digested with sulphuric acid to fuming as by Thompson & Bremner (1935*a*). This procedure is very time consuming and would have been impossible in a temporary laboratory such as that used at Newlyn for the present investigation.

'Total' iron as determined. The original method was modified precisely as that for reducible iron. Compounds of iron were broken down by boiling with acidified bromine water. This method sets free only 41% of the iron in a solution of Waksman's ferrolignoprotein in sea water, whilst the method for reducible iron will liberate 20–25%. In sea water, therefore, there may well be organic compounds which are resistant to this treatment and terrigeneous clay and mineral particles would certainly be so. None the less, the method measures a definable quantity, is quick, and with occasional recourse to a service gas-mask may be used in a laboratory not equipped with a fume chamber.

The evaluation of the correction terms and of random analytical errors is given in Appendix I.

MIDWINTER RESULTS, 1946–47

A temporary analytical laboratory was set up at Newlyn, the most westerly fishing port in Cornwall, and occupied between 1 and 28 January 1947. During that period the Marine Biological Association's research vessel *Sabella* made her base there with Mr P. G. Corbin as scientific officer in charge of work at sea. The data on the distribution of salinity, temperature, phosphate, silicate and zooplankton will be published separately. Fig. 1 shows the position of the stations worked for iron samples; fuller details will be presented in the paper dealing with phosphate. A preliminary cruise was also made on 4 and 5 December 1946.

The results are set out in detail in Table II. Triplicate analyses did not agree. Moreover, the distribution of iron at the bottom was markedly different from that in the water between the surface and 50 m. The dispersion of all results for reducible and for total iron may be seen from Fig. 2 in which all separate analyses have been grouped in arguments of 5 mg.-atom/m.^{3} Fe × 100 or 'units'. The distribution of analyses of inorganic phosphate constructed with the same argument was utterly different. The relatively few analyses for bottom water showed a very wide spread.

Much of the iron must be distributed very differently from inorganic phosphate and nitrate. The latter, except for a little ferric phosphate (see below), are truly dissolved in the water, are vertically uniformly distributed under uniform isothermal, isohaline conditions and usually show complete uniformity within a small sample.

At station A3 (= International Hydrographic Station E2) on 7 January, the weather was very heavy, no nets could be worked, the sounding of 110 m. was at least 15 m. too great and the angle on the warp when sounding and when sampling at 50 and 80 m. nominal depth was estimated at 35–40°. Whether this weather was the cause or not, the results were highly anomalous, and have had to be omitted from the statistical examination of all samples taken at standard depths, presented in detail in Appendices II and III and summarized in Table III.

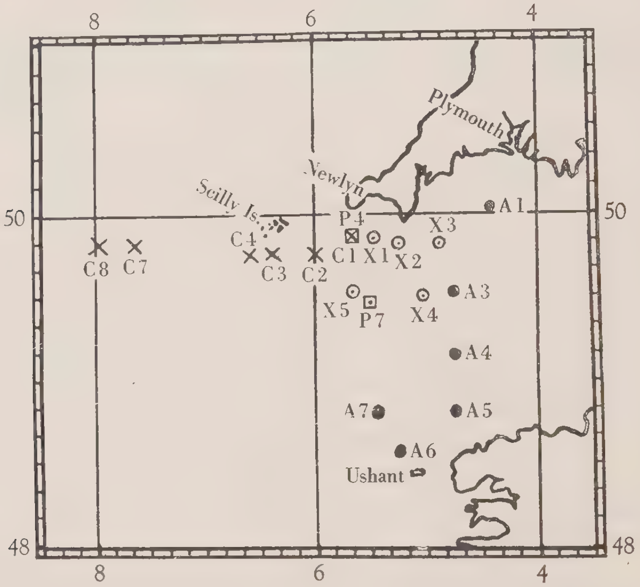

Fig. 1. Station positions. Cruise P, 4–5 December 1946. Cruise A, 6–7 January 1947. Cruise C, 17–18 January 1947. Cruise X, 21–22 January 1947. Equivalent international (E) stations: E1=A1, E2=A3, E3=A6, E7=P4=C1, E25=C4.

Within the upper layers, analyses of both total and reducible iron at different depths (5, 25 and 50 m.) show no significant variation either in mean values or in the variation as shown between analyses. The whole of the variability of the total iron appears to be due to the reducible iron component. The difference of 6 units may be attributed to a dispersed unreducible fraction with a standard deviation not differing significantly from zero. There is present therefore a small dispersed fraction detectable only when the water has first been oxidized with bromine water. It is most probably in organic combination and under the conditions prevailing in January 1947 must have been present in the bottom water in like amount. The analytical data require only that this unreducible fraction shall be well dispersed in the water. It does not necessarily require it to be truly dissolved.

Table II. Total and Reducible Iron in the English Channel, December 1946 to February 1947 as mg.-atom/100 m.^{3} Fe, referred to in the Text as 'units'. Volume analysed throughout was 150 ml.*

Station and sounding (m.)	Depth (m.)	Reducible iron	Total iron
	Cruise P, 4–5 December 1946		
P4 (=E7)	0	—	17
(76 m.)	5	9	—
	25	7	20
	50	22	26
	70	12	64
P7	0	27	19
(104 m.)	5	16	7
	25	9	10
	50	9	24
	70	14	53
	100	27	28
	Cruise A, 6–8 January 1947		
A1 (=E1)	5	—	37, 25, 18
(78 m.)	25	—	28, 32, 14
	50	—	39
	70	—	130, 73, 10
A3 (=E2)	5	—	6
(110 m. observed,	25	—	93
91 m. by chart)	50	—	6, 76
	80	—	69
A4	5	—	10
(94 m.)	25	—	7
	80	—	53
A5	5	—	34
(104 m.)	25	—	36
	50	—	26
	95	—	—
A6 (=E3)	25	—	0
(111 m.)	50	—	6
	75	—	28
	100	—	8
A7	0	—	23
(112 m.)	5	—	30, 21, 36
	25	—	31, 39, 32
	50	—	33
	75	—	36
	100	—	189, 26

* Though the results are given in terms of mg.-atom/100 m.^{3}, they are proportional to, and may be regarded equally as representing, weights of iron in single 150 ml. samples. For statistical purposes they are treated as such. For much of the development to follow, the distinction though subtle is fundamental. Mg.-atom/100 m.^{3} are equivalent to 0·8376 μg. per 150 ml. The very slight difference between the litre and the cubic decimetre is ignored.

TABLE II (*cont.*)

Station and sounding (m.)	Depth (m.)	Reducible iron	Total iron
Cruise C, 17–18 January 1947			
C1 (=E7=P4)	5	—	8
(73 m.)	25	—	38
C2	60	—	26
(95 m.)	85	—	78
C3 (=N2)	0	—	24
(98 m.)	5	—	24
	50	—	42
	75	—	54
	90	—	68
C4 (=E25)	0	—	41
(100 m.)	25	56, 16, 12	32
	50	24, 8, 19	28, 10, 29
	75	6, 23, 12	38, 52, 78
	90	18, 8	22, 6, 24, 37
C7	0	—	15
(130 m.)	5	—	14
	25	—	20
	50	—	20
	120	—	64
C8	25	—	13
(127 m.)	50	—	16
	90	—	17
Cruise X, 21–22 January 1947			
X1	0	—	25
(86 m.)	5	17	19
	25	20	34
	50	—	24
	75	79	44
X2	25	—	35
(90 m.)	50	—	30
	75	—	67
X3	0	20	—
(80 m.)	5	26	30
	25	29	52
	50	19	41
	75	37	36
X4	0	—	21
(100 m.)	5	19, 16, 12	24, 29, 32, 25
	25	10, 7, 10	22, 34, 16
	50	32, 43, 0	27, 16, 33
	90	0, 0, 0	8, 11
X5	0	53	—
(103 m.)	5	28	49
	25	4	19
	50	—	20
	95	—	52
27 February 1947 (compare Appendix I, Table XIII)			
E1	5	7·4±3·0	—
(71 m.)	25	14·1±9·3	—
	67	11·6±3·5	—

In the bottom water the mean content of reducible iron is rather less than in the upper layers but the difference is not statistically significant. Within the error of observation, with limited numbers of analyses, the reducible iron is randomly distributed throughout the whole water column. There is no significant variation with depth.

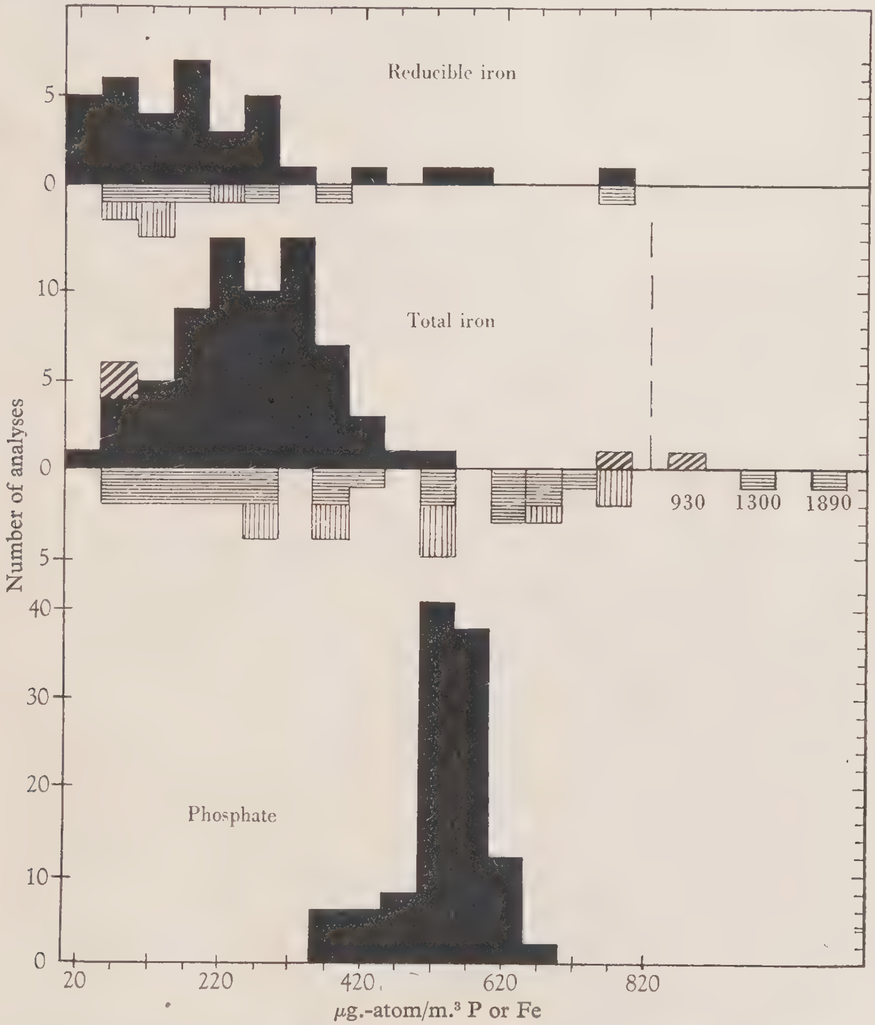

Fig. 2. Midwinter 1946–47. Numbers of iron and phosphate analyses grouped in classes with an argument of 50 μg.-atom/m.³. (The first class comprises analyses of 0, 10, 20, 30 and 40 μg.-atom/m.³, and is graphed as the median, 20 μg.-atom/m.³; and so on.) The iron analyses are separated as follows: *black*, samples from the upper water layers (between 0 and 50 m.); *horizontal hatching*, samples from bottom water; *vertical hatching*, samples from intermediate layer (23–37 m. above bottom). The upper water samples from station A3 are *cross-hatched*.

By contrast the mean content of total iron in the bottom water is twice as great as in the upper layers. The disparity in the standard deviation is even greater (3·5/1). This increase in the total iron content of bottom water has been shown to be due neither to the reducible nor to the dispersed unreducible fraction. It can be due only to a coarsely particulate unreducible fraction present only in the bottom water, amounting to 32 units with the very large standard deviation of 36 units. Since this fraction is only set free after oxidation with bromine water it is probably contained in particles of organic detritus stirred up from the bottom deposits by turbulent water movements.

TABLE III

	Upper layers (0–50 m.)		Intermediate layer (60–75 m.)		Bottom layer	
	No. of analyses	Mean and S.D.	No. of analyses	Mean and S.D.	No. of analyses	Mean and S.D.
Total iron	68	25 ± 11	8	46 ± 17	23	51 ± 38
Reducible iron	31	19 ± 14	4	14 ± 9	8	13 ± 14
Dispersed unreducible iron (max.)	—	6	—	6	—	6
Coarsely particulate iron (min.)	—	0	—	26 (± 15)	—	32 (± 36)

The few samples from 'intermediate' depths (60–75 m. depth and 23–37 m. above the sea-bed) reveal the same story but, since the standard deviation of the particulate unreducible fraction is less (± 15 compared with ± 36 units), the average size of the particles must also be less than nearer the bottom. There is therefore a vertical gradient in particle size from the upper layers towards the bottom. The density of the water column in January 1947 was uniform; consequently to attain such a distribution these particles must have been slightly heavier than water.

The bottom (75 m.) analysis for reducible iron (79 units) at station X1 has been omitted from the statistical examination but, none the less, it seems to have meaning. The 150 ml. sample must have contained one or possibly two large particles containing 0·1 μg.-atom of reducible iron. Such a particle would almost certainly be suitable chemically for direct assimilation by plants; physically it must be far too large to be handled by any single cell for it would be sufficient to meet the needs of a strong growth of phytoplankton in many litres of water. The part played by such particles cannot at present be fairly assessed.

To sum up, the bottom water contained:

(*a*) A well dispersed unreducible organic iron fraction amounting to about 6 units.

(*b*) A particulate reducible fraction amounting to about 13 units. This was probably flocculent ferric hydroxide or phosphate.

(*c*) A coarsely particulate or detrital unreducible fraction amounting to about 30 units.

(*d*) Occasional relatively large particles containing much reducible iron.

Ferric hydroxide or phosphate, precipitated, flocculated or excreted at mid-depths, will be caught by filter-feeding zooplankton, adsorbed upon phytoplankton or will settle slowly to the bottom. There, turbulence due to tides, currents and other water movements tend to keep these particles in intermittent movement. Sessile and free-swimming animals feeding on and near the bottom will also add their quota of iron-containing faeces. During passage through the intestines of filter feeders, some of the iron may be dissolved by acid digestive juices and excreted in solution whilst some will become incorporated in an organic matrix of mucilage and waste products which, after excretion, will tend to be broken down by bacteria so dispersing the iron in finer particles. The distribution of iron amongst these several fractions in the bottom water therefore must provide the key to the return of iron into circulation in shelf waters.

The earlier diatom outbursts in coastal areas believed by Gran (1931, 1933) to be due to iron derived from the land could equally well be ascribed to iron derived by vertical mixing from such an iron-rich layer of bottom water on a shelf. A heavy storm should increase the iron content of the photosynthetic layers at the expense of the bottom water and deposits. This may be the meaning of the very high and erratic results at station A3 (cf. Fig. 2).

Possible Removal of Particulate Iron from Bottom Water by Molluscs

Station X4 (49° 30′ N., 5° 00′ W.) is unique, for there in the bottom water triplicate analyses failed to detect any reducible iron, total iron was very low (the duplicate analyses of 8 and 11 units being 15 units less than in the overlying water) whilst the phosphate distribution indicates active removal of particulate ferric phosphate from the water (p. 299). Nothing remotely like this was found at any other station; that this water was of 'south-western' origin is no explanation. The absence of particulate matter near the bottom called to mind the conditions in the mussel-purification tanks at Conway, North Wales, when the molluscs placed in turbid estuarine water have been actively at work for a few hours. No physical cause for the state of affairs at station X4 is to be seen so that the conclusion that the water had been clarified by a large population of bottom suspension feeders seems the only reasonable alternative.

Mr H. P. Sherwood (private communication) at Conway placed a single mussel at the bottom of a litre-measuring cylinder about 0·4 m. high and covered it with a thick suspension of red oxide (Fe_2O_3) in estuarine water. In 1 hr. the mussel had cleared much of the suspension from the water whilst in 2 hr. no trace of the opacity could be seen. Given a certain amount of tidal mixing a bed of mussels should have no difficulty in the course of a few days in clarifying a bottom layer of water 5–10 m. thick.

Mussels do not live at a depth of 90 m. but, according to Mr G. A. Steven, an organism with similar feeding habits, the large mollusc, *Pinna*, does.

Capt. Creese of the Laboratory's research vessel *Sabella*, when asked where he would look for *Pinna*, gave a ground including the position of station X4 and no other position investigated during the winter cruises. Furthermore, on 20 July 1936 at station 1, well within this ground, zero reducible and total iron was found at the bottom (Table V). If a bed of molluscs, such as *Pinna*, does have such a marked effect on the iron content of the bottom water, further lines of investigation would open up. Acting over a period of time the molluscs would strip the iron from the water column, converting it first into faeces and much pseudo-faeces which would tend to accumulate in bottom deposits and return only slowly to the water. Failing replenishment by water from areas outside the beds, the surface flora would in time be adversely affected both qualitatively and quantitatively by shortage of iron. Thus, in certain hydrological circumstances, an inverse relationship may develop between a dense bottom molluscan fauna and the phytoplankton production many metres above. Such an area may prove to be adverse to early spring outbursts of phytoplankton (cf. p. 287).

DISTRIBUTION AND SIZE OF LARGE PARTICLES OF FERRIC HYDROXIDE

The whole of the variability of total iron in the uppermost 50 m. appears to be due to the reducible fraction composed, presumably, of flocks of ferric hydroxide and phosphate. In January 1947 it amounted to 19·3 units (mg.-atom/m.^{3} × 100) (p. 310). The dispersed unreducible fraction (6 units) contributed little to the variance[1] of total iron for which most analyses are available. However, the variance for neither total nor reducible iron as calculated in Appendices II and III is appropriate for calculating the average size and numbers of the particles, since variation between stations would be included. Eight samples drawn from between 0 and 50 m. had been analysed in triplicate or quadruplicate for total iron, viz. A1, 5 m.; A1, 25 m.; A7, 5 m.; A7, 25 m.; C4, 50 m.; X4, 5 m.; X4, 25 m. and X4, 50 m. For these there are twenty-five analyses on sub-samples, eight means and seventeen degrees of freedom, the variance between subsamples being 64·8 square units (p. 310).

A fair estimate of the variance introduced by the chemical technique is to be had from Appendix I, Table XIII. The standard deviation of 3·08 units for station E1, 25 m. Series 1 corresponds to a variance of 9·5 square units. Therefore 64·8 less 9·5 (= 55·3) is the final estimate of the variance between different readings of total iron from one position in the water column when the size of each water sample is 150 ml. That is, 55·3 represents the sampling variance for iron in a volume of 150 ml. of sea water in the western English Channel in January 1947. Furthermore, the amount of iron subjected to this sampling variance is 19·3 units. A variance of such magnitude (55·3), it would seem, can arise only because the iron is aggregated in particles. Two questions may be posed: (1) how many particles are there? and (2) what is their size expressed in terms of their iron content?

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[1] The limitation that the variance applies only to the sample volume of 150 ml. needs constantly to be borne in mind, e.g. it is not a function of the cubic metre.

According to Mr G. M. Spooner (private communication) random variation in numbers of particles dispersed in a volume of fluid (of which they form an insignificant fraction) may be expected to conform to the Poisson distribution.

The Poisson frequency distribution is a special limiting case of the binomial distribution, derived from the binomial expansion $(p+q)^n$, when p is a very small fraction but n correspondingly large so that np remains an ordinary number. In our example the volume of water is regarded as an aggregate of a large number (n) of particle-sized units, of which a small proportion (p) belong to the special iron-containing particles under investigation, the rest, a proportion q, to the medium. The mean number of iron-containing particles in the given volume is np. The variance amongst different samples is also np, since the general binomial variance of npq becomes np when q is not significantly different from unity. It is a characteristic property of the Poisson distribution that the Mean and Variance are equal. Identical values should therefore be obtained for the mean and variance when these are expressed as numbers of particles instead of as weights of iron per unit volume.

In the present instance the mean is 19·3 units of iron and the variance 55·3 sq.units. If it is supposed that the iron is distributed in a number of equal aggregates or particles, it at once follows that 55·3/19·3 (=2·865 units) represents the amount of iron per particle. (Converting by the factor given in the footnote to Table II this equals 0·240 μg. per particle.) There will thus be a mean number of 19·3/2·865 (=6·74) particles per 150 ml. This is equivalent to 45 particles per litre. This estimated mean number will scarcely be affected even if there is an appreciable range of variation in either particle-size or in iron-content of particles. An assessment of the accuracy of this result, not rigorously statistical, suggests that the number of particles could just possibly have been as low as 30 or as high as 80 particles per litre and almost certainly was not outside these limits.

To arrive at a rough estimate of the size of such a particle let us assume it to have a specific gravity of 1·1 and an iron content of 10%. Such a particle would occupy

$$\frac{0{\cdot}24 \times 10^{-6} \times 10}{1{\cdot}1} = 2{\cdot}18 \times 10^{-6} \text{ c.c.}$$

If the particle is spherical and of radius r, then $r = 0{\cdot}08$ mm.

That is, there were about 45 large particles per litre of water with a diameter averaging about 160 μ. If the iron content had been assumed to be $1\frac{1}{4}$% instead of 10%, this diameter would have worked out at 320 μ.

The result means that in the sea water of the English Channel between the surface and 50 m. at midwinter in 1946–47 four-fifths of the iron was associated with a very few large particles. We have to ask ourselves whether such a surprising result is possible and what such particles might be.

No collections for phytoplankton were made but, during the first two cruises, Mr P. S. B. Digby was on board and made some quantitative collections between 50 m. and the surface for his studies upon copepods. He used a Harvey quantitative net with 120 meshes per linear inch. Such a net would catch most, though not all, of the particles of the size we are considering. Two of these catches were generously placed at my disposal and Dr T. J. Hart has kindly examined them for me. In the catch from station C4 he found 45 'large particles' per litre which had diameters of the order of $100\,\mu$. This number is minimal and half made up by partially disintegrated colonies of *Phaeocystis*. In the catch from station A7 he was able to find only nine such particles per litre; nearly half were faecal pellets whilst a quarter were cells of the alga *Halosphaera viridis* (average $120\,\mu$).

That diatoms may heavily adsorb ferric hydroxide and phosphate is known (Harvey, 1937*a*) but whether these particles did in fact contain sufficient iron to account for our analytical findings is not known. The material was collected for very different ends and no exact agreement could be expected. All that can be said is that particles in sufficient numbers and of the right size were present to make the analytical results not unreasonable.

As the spring advanced the numbers of large diatoms, of large herbivores and of their faecal pellets must have increased rapidly. The number of smaller organisms also would have increased. The iron associated with living matter must have passed through many cycles in the course of the spring, though only a small part may have been truly metabolized by plants or animals. The iron would have become distributed amongst a larger and larger number of organisms and faecal pellets whilst the percentage content of each one, on an average, would have become less and less. So far as iron is concerned, this is equivalent to more and smaller particles. With about 370 particles or organisms per litre the variance would become about 1 sq.unit and any possibility of establishing the presence of particulate iron by statistical study of replicate chemical analyses would vanish. There is therefore less chance of establishing the thesis in these waters at seasons other than midwinter.

Between 9 March and 14 November 1934, analyses of iron were carried out upon catches made at station L4 with the Harvey quantitative net (200 meshes per linear inch). The maximum iron content was found on 20 March coincident with the phytoplankton maximum, 41 μg.-atom per cu.m. of water filtered ($\equiv 4{\cdot}1$ units) (Harvey *et al.* 1935; Cooper 1935). During the next fortnight the plankton-iron fell to one-third whereas the plankton-phosphate remained almost constant. As the spring advanced the ratio of iron to phosphate expressed in gram-atoms fell from 2·55 to 0·45, whilst during the autumn it rose from 0·48 to 1·93 on 14 November. It is likely therefore that at midwinter the ratio would have been still higher. None the less, the gap between the observed maximum of 4·1 units caught with the Harvey net on 20 March 1934 and 19·3 units indicated by the present study at midwinter 1946–47 is a large one to bridge.

The analytical method has been tested under conditions where the iron has intentionally been kept as highly dispersed as possible. There is evidence, not consistent enough to publish, that if an iron solution, ferric or ferrous, is added to sea water at its natural pH around 8·1, some of the added iron becomes undeterminable. Results agree poorly. Possibly some iron flocculates, though not visibly to the naked eye, and the method does not quickly attack these flocks (cf. Buch, 1942). If flocks or ferruginous particles are present analytical errors may be exaggerated, whereas with well-dispersed iron they will not arise. In such case, the general picture outlined here is correct but the variances may have been somewhat exaggerated so that the iron in the sea may have been distributed amongst more and somewhat smaller particles than the present study has suggested.

THE HORIZONTAL DISTRIBUTION OF IRON

The horizontal distribution of phosphate or other truly dissolved nutrient is best studied in terms of the integral mean content of the vertical water column which takes account of the unequal spacing of standard depths (Cooper, 1933, p. 722, as 'average nutrient salt content of the water column'). For a randomly distributed constituent such as total iron, this integral mean would have value only if arithmetic means of a large number of analyses were first available at each depth and station. The most convenient measure of the total stock of iron in the English Channel in winter is therefore the simplest, the arithmetic mean of all analyses at a station irrespective of depth. No clear picture emerges from charting single stations, but one can be obtained by arranging the data for stations at which iron and phosphate analyses are both available in three groups of increasing phosphate content (Table IV, fourth column).

TABLE IV. RATIO OF TOTAL IRON TO PHOSPHATE

(Mg.-atom/$m.^3$ Fe and P × 100)

	No. of analyses		Phosphate integral mean for whole water column		Total iron			
No. of stations n_1 (1)	P (2)	Fe n_2 (3)	Range (4)	Average for n_1 stations (5)	Arith. mean of n_2 detns. (6)	S.D. (7)	S.E. of mean (8)	Ratio: Fe/P (9)
5	23	29	**37–50**	43·4	24·9	14·0	2·6	0·57
6	39	33	**51–55**	53·2	28·7	18·3	3·2	0·54
5	27	35	**56–63**	59·4	35·7	15·0	2·5	0·60

The standard error of the means (col. 8) shows that the increase in total iron with phosphate given in the sixth column is just statistically significant. The inclusion of bottom analyses somewhat increases the standard deviations (col. 7) compared with those for 0–50 m. in Table XIV. The ratios of total iron to phosphate (arithmetic mean average of integral means) (col. 9) are not far from constant. The analyses of the midwinter maximum of phosphate therefore gave a measure of the statistical probability of occurrence of total iron (0·57 × concentration of phosphate). At any one station the total iron calculated from this ratio is as likely to represent the total iron content as the limited number of analyses actually performed.

For computing Table IV, stations C1 and C2 were treated as one and, in addition to station A3 (p. 282), the analyses at A1, 70 m. (130 units) and A7, 100 m. (189 units) were omitted. These analyses were grossly at variance with replicates and their inclusion, whilst increasing the spread of the mean of total iron in the fifth column, nearly doubles the standard errors of the mean in the two higher groups. Both analyses were on bottom water making it likely that single particles of bottom detritus of very high iron content were caught by the bottle; both are better left out.

THE DISTRIBUTION OF IRON IN 1933–34

When the 1933–34 work was reported (Cooper, 1935), the reason for the erratic results obtained was not clearly understood and to economize space figures for the average content of the water column only were presented. Though the data are not sufficiently homogeneous for a satisfactory statistical study, further information of value for the present account may be had from them.

(1) On 15 December 1933, at all the stations between L1 and L5 (Eddystone) and at E1, the total iron content of surface water sampled *with a wooden bucket* was high (32–43 units), whilst that at 5, 50 and 69 m. was a mere 7–9 units suggesting that about 30 units was in some way associated with the surface layer.

(2) On 12 February 1934 at stations L4, L6, E1 and at a position midway between E1 and E2 erratic results were obtained, the surface results for total and reducible iron being especially erratic and high.

(3) On 20 March 1934 at the peak of the spring outburst at L4 surface total iron was higher by 54 units than in deeper water whilst at E1 the water at 5 m. contained none. Thence to the bottom there was a graded increase to the very high bottom content of 54 units. At all depths reducible and total iron were identical. Clearly the diatoms had stripped the water in their zone of growth of iron which had found its way to the bottom in a readily attackable form.

THE SURFACE FILM OF FERRIC HYDROXIDE

In 1933–34 concentration of iron in the surface layers was frequent. Yet at midwinter 1946–47 statistical examination showed no such surface concentration. The answer to this contradiction arises from the different methods of surface sampling used in the two years. In 1946–47 all surface samples were taken with the Nansen-Pettersson water-bottle submerged just beneath the surface and not breaking water. It sampled the uppermost metre of water but not the surface film. The wooden bucket used throughout 1933–34 definitely included an area of the surface film to which it is therefore reasonable to attribute the high surface results in that year.

Harvey (1937*b*) has shown that an unprotected sol of ferric hydroxide in sea water is electropositive whilst a similar sol protected by gum arabic is electronegative. A sol afforded definite protection by albumen carried either no charge or one too small to be measured with the apparatus employed. Mokrushin (1947) has found that on ageing colloidal solutions of positively charged ferric hydroxide a very thin invisible surface film is formed spontaneously by coagulation, whereas no such film is formed on sols of negatively charged ferric hydroxide. From these and many other observations he has concluded that this surface coagulation of electropositive sols results in the formation of a uni-micellar film, at first only a network—later becoming a compact solid film. The thickness of this layer of ferric hydroxide was 3–4 $m\mu$ and it was further deduced that micelles in the hydrosol were lamellar or plate-like with a diameter of 30–40 $m\mu$. One such micelle would weigh about 10^{-17} g. and cannot be identified with the particles already discussed. A solid film of ferric hydroxide, 1 sq.cm. in area, 3·5 $m\mu$ thick and having a specific gravity of 3·5 would weigh 1·0 μg.

The wooden bucket used for surface sampling was about 30 cm. in diameter and was usually filled to a depth of about 20 cm. or a volume of 14 l. If we suppose that (*a*) the sea surface was uniformly covered with such a uni-micellar layer, (*b*) that a disk of the surface 30 cm. in diameter (containing $\pi \times 15^2 \times 1{\cdot}0\,\mu\text{g.} = 700\,\mu\text{g.}$ ferric hydroxide) was sampled by the bucket and (*c*) that pouring from bucket to storage bottle led to fair sampling of the superficial and bulk phases, then 700 μg. ferric hydroxide would have become distributed in 14 l. of water. That is, each litre would appear to contain 50 μg. ferric hydroxide or 0·47 μg.-atom of Fe. This figure gives a rough maximum for the amount of iron present in a sample taken from the surface by dipping up with a bucket and attributable to a surface unimicellar film of electropositive unprotected ferric hydroxide. The results of 15 December 1933 would agree with two-thirds of the surface of the sea being covered by such a film. Naturally only the order of magnitude of this calculation has significance, but its essential soundness is supported by Dr W. R. G. Atkins's observation (private communication) that the iridescent 'oily' film frequently observed on bog ponds consists largely of ferric hydroxide. This is apparently well known to limnologists.

TABLE V. HYDROLOGICAL DATA, CRUISE OF 20–22 JULY 1936

Station no.	Position	Date and time (G.M.T.) July	Depth (m.)	Temp. (° C.)	Sal. (‰)	PO$_4$-P (mg.-atom/m.^{3} × 100)	Iron (mg.-atom/m.^{3} × 100)			
								Reducible		
							Total	Unfiltered water	Membrane filtered at pH 8	Membrane filtered at pH 4
1	50° 08′ 30″ N.,	20,	10	13·4	34·50	4	4	4	—	—
	4° 39′ 30″ W.	1415	65	10·9	34·59	19	0	0	—	—
2	49° 56′ N.,	20,	10	11·65	34·67	16	13	9	—	—
	5° 13′ W.	1750	60	11·6	34·70	39	2	2	—	—
3	49° 47′ N.,	20,	10	13·4	34·80	9	4	4	—	—
	5° 22′ 10″ W.	2000	85	11·52	35·18	31	23	23	—	—
4	49° 29′ 40″ N.,	20,	10	15·57	34·99	6	21	0	—	—
	5° 38′ 20″ W.	2330	80	11·28	35·28	31	0	0	—	—
5	49° 13′ 20″ N.,	21,	10	15·57	34·97	5	38	9	—	—
	5° 54′ 30″ W.	0310	90	11·0	34·39	56	36	11	—	—
6	49° 08′ 20″ N.,	21,	10	15·0	34·98	4	23	9	—	—
	6° 24′ W.	0655	100	10·71	35·44	45	43	11	—	—
7	49° 25′ 40″ N.,	21,	10	15·25	34·92	5	16	16	—	—
	6° 9′ 30″ W.	1040	100	10·87	35·34	38	18	9	—	—
8	49° 43′ N.,	21,	10	14·3	34·99	3	18	9	—	—
	5° 55′ W.	1410	80	11·1	35·32	32	21	30	—	—
11	50° 2′ 30″ N.,	22,	0	15·0	34·45	6	16	2	0	16
	4° 26′ 40″ W.	1220	5	14·1	34·45	6	16	2	0	9
			10	13·15	34·47	7	18	4	0	4
			25	11·85	34·61	24	2	2	0	2
			50	—	34·58	24	9	0	0	0
			65	11·29	34·56	24	0	0	0	2

THE DISTRIBUTION OF IRON IN JULY 1936

In July 1936 a cruise was made by S.S. *Salpa* to the southward of the Scilly Isles with Mr F. S. Russell and Mr P. H. T. Hartley on board. Ten stations were worked with the young fish trawl and eight with the Nansen-Pettersson water-bottle at 10 m. and near the bottom. The temperature, salinity (analyses by the Government Chemist), inorganic phosphate and reducible and total iron determined on the water samples, are given in Table V. Station 11, about 3 miles to the westward from the position of station E1, was worked for a full hydrographical depth series, but not for the young fish trawl.

Since there was a strongly marked thermocline throughout the area except at station 2, no physical or chemical resemblance need be expected between the water at 10 m. and that at the bottom. The young fish trawl may sample both layers and, in any event, the two species of *Sagitta*, of such value in characterizing water masses in the area, migrate daily across the thermocline. One species though perhaps initially associated with only one layer may become apparently associated with both. It is necessary, therefore, to compare the *Sagitta* distribution with the hydrological data for both layers separately.

(*a*) *Comparison in Bottom Waters*

The bottom waters may be divided into three clearly contrasted groups (Table VI).

TABLE VI. HYDROLOGICAL OBSERVATIONS AT THE BOTTOM ON 20–22 JULY 1936 COMPARED WITH CATCHES OF *SAGITTA*

Sal. (‰)	Station	Depth (m.)	Phosphate (mg.-atom/m.^{3}P × 100)	Iron (mg.-atom/m.^{3} × 100)		*Sagitta*	
				Reducible	Total	*elegans*	*setosa*
Low salinity group:							
34·56	11	65	24	0	0	Not determined	
34·59	1	65	19	0	0	92	11
34·70	2	60	39	2	2	342	12
Medium salinity group:							
35·18	3	85	31	23	23	5	1
35·28	4	80	31	0	0	284*	0
35·32	8	80	32	30	21	0	0
35·34	7	100	38	9	18	54	0
High salinity group:							
35·39	5	90	56	11	36	970*	0
35·44	6	100	45	11	43	4110	0

* Night stations.

Low salinity group. Three stations of very low salinity extending right to the bottom, relatively low phosphate, very low or zero reducible and total iron and a few *Sagitta setosa*. *S. elegans* was present in numbers exceeding *S. setosa*.

Medium salinity group. Four stations with bottom salinity about 35·3 ‰, intermediate content of phosphate and of reducible and total iron and only a single *S. setosa*. *S. elegans* was present at three of the stations.

High salinity group. The two most westerly stations with salinities 35·39 and 35·44 ‰ had high phosphate and total iron, a large difference between reducible and total iron (28 units), no *S. setosa* and a great many *S. elegans*. These last stations were evidently occupied by truly 'elegans' water. Their high unreducible iron content supports the 1946–47 midwinter results in showing 'elegans' water to be relatively rich in this form of iron at the bottom.

(*b*) *Comparison of* 10 *m. Observations*

The 10 m. results are most conveniently arranged in ascending order of total iron content (Table VII). It will be seen than low total iron is associated with the lower salinity water and presence of a few *S. setosa*. Relatively high total iron is associated with higher salinity water, complete absence of *S. setosa* and includes the stations with large catches of *S. elegans*. Reducible iron and phosphate tell little, but as far as a correlation can be seen low total iron marches with low reducible iron and relatively high and erratic phosphate, high total iron with relatively high reducible iron and uniformly low phosphate (3–6 mg.-atom/m.³).

TABLE VII. HYDROLOGICAL OBSERVATIONS AT 10 M. DEPTH ON 20–22 JULY 1936 COMPARED WITH CATCHES OF *SAGITTA*

Iron (mg.-atom/m.³ × 100)				*Sagitta*		
Total	Reducible	Station	Salinity (‰)	*elegans*	*setosa*	Phosphate (mg.-atom/m.³ × 100)
Low total iron and salinity group:						
4	4	3	34·80	5	1	9
4	4	1	34·50	92	11	4
13	9	2	34·67	342	12	16
18	4	11	34·45	Not determined		6
High total iron and salinity group:						
16	16	7	34·92	54	0	5
18	9	8	34·99	0	0	3
21	0	4	34·99	284*	0	6
23	9	6	34·98	4110	0	4
38	9	5	34·97	970*	0	5

* Night stations.

The fresh water which had reduced the salinity of the stations nearer Plymouth had in no way enriched the store of iron; there the slender stock of iron was all reducible. The typical 'elegans' water at 6° W. was much richer in both total iron and phosphate but the additional iron was mostly unreducible.

The complete vertical series at station 11 near E 1 is of interest. In one set of analyses the sea water was brought to pH 4 (required acid determined by titration with bromophenol blue as indicator to an end-point matched against the same indicator in M/20 potassium hydrogen phthalate) and left for 30 min. before filtration through a collodion membrane of filtration time 20 sec. Whereas membrane filtration at pH 8·1 removed all the iron, at pH 4 part had become dissolved and passed into the filtrate. Again nearly all the iron, in marked contrast to phosphate, had become concentrated above the thermocline. This partition of iron upwards is difficult to understand on physical grounds.

Comparable Results from North American Waters

Rakestraw, Mahncke & Beach (1936) filtered a number of samples through Whatman No. 42 filter paper and then analysed the content of iron by co-precipitation of ferrous sulphide with magnesium hydroxide. Water from the Gulf of Maine, all collected in summer, contained very little iron; usually it was zero. Positive results (8–20 units) were, however, found on a number of surface samples, but whether these included the surface film or were more truly 0·5 m. samples is not stated. Filtered samples from four deep stations in the Atlantic Ocean off New England were also analysed. Here also there was a tendency for surface results to be high and at other depths ranging from 50 to 3830 m. iron was always detectable (2–25 units). Thompson & Bremner (1935*b*), 25–100 miles off the continental shelf in the north-east Pacific, obtained very similar results for 'soluble' iron, i.e. iron which had passed a Whatman no. 42 filter paper. Seiwell (1935), by a method which included iron in detritus and organisms trapped in the water-bottle and is similar to the method for 'total' iron of the present paper, examined waters collected in December and August, also from the Gulf of Maine. The distribution there in December 1933 was similar to that in the English Channel in December–January 1946–47. For two stations at which phosphate analyses were also made (Conseil International, 1933) the total-iron/phosphate ratio may be worked out. At station 1880 (42° 45′ N., 68° 48′ W.) on 6 December 1933, the uppermost 50 m. showed uniform distribution of salinity (33·06 ‰), temperature (7·14° C.) and phosphate (99 units) and high and *variable* iron content yielding a Fe/P ratio ranging from 0·67 and 0·91. In the underlying water of markedly different structure, this ratio was only 0·44. A position 70 miles to the eastward at station 1897 (42° 25′ N., 67° 06′ W.) was characterized by a very much lower ratio (0·13–0·25), not notably affected by a marked discontinuity at 100 m. Comparable English Channel ratios are summarized in Table IV. It is evident that the relative abundance of iron and phosphate varies in different parts of the world much more than do nitrate and phosphate.

Particulate Ferric Phosphate

Occasionally in phosphate analyses, results are obtained which appear high compared with those from adjacent positions, vertically and horizontally. Contamination, or the widely recognized difficulties inherent in methods involving complex molybdates, provide explanations ready to hand. Routine calibration runs to determine salt error in phosphate analyses are now made in triplicate to enable 'untrustworthy' results to be rejected. It would now seem that these causes have been invoked too frequently, at any rate by the writer, to explain what is a truly variable property of the sea water itself.

Harvey (1937*a*) has pointed out that ferric phosphate as well as hydroxide is likely to be present in sea water in particulate form. If the distribution of ferric phosphate is as erratic as that of total iron, we should have an explanation of these 'untrustworthy' phosphate analyses. Cruise X provided several such, with vertical variations greater than would be anticipated in isothermal, isohaline water in unsettled weather. Let us assume that dissolved inorganic phosphate was indeed vertically uniformly distributed under the isothermal conditions obtaining and was represented by the smallest analysis found in each vertical series. Phosphate in other samples or sub-samples in excess of this smallest value would then represent particulate ferric phosphate randomly distributed. Although there is no clear correlation between this and the total iron content, one may be found with the total iron in excess of the smallest analysis for total iron found for each vertical series. Table VIII shows the first step in the calculation for station X4.

TABLE VIII. APPROXIMATE CALCULATION OF PARTICULATE FERRIC PHOSPHATE AT STATION X4

(mg.-mol./m.^{3} $FePO_4 \times 100$) or (mg.-atom/m.^{3} Fe or P × 100)

				Total iron			
Depth (m.)	Phosphate found	Assumed dissolved phosphate	Particulate $FePO_4$	Found	Mean	Smallest analysis	Excess over smallest analysis
0	40·0	37·1	2·9	21	21·0	8	13·0
5	39·1	37·1	2·0	24, 29, 32	28·3	8	20·3
25	43·5	37·1	6·4	22, 34, 16	24·0	8	16·0
50	44·3, 42·2	37·1	7·2, 5·1	27, 16, 33	25·3	8	17·3
90	37·6, 37·1, 37·3	37·1	0·5, 0·0, 0·2	8, 11	9·5	8	1·5

The 'particulate $FePO_4$' (col. 4) found in this way from all separate phosphate analyses for the five Cruise X stations respectively were then arranged in groups of increasing $FePO_4$ content and compared with the corresponding mean 'excess total iron' figures (as in the last column of Table VIII). The result of the calculation is set out in Table IX. Figures such as the duplicate phosphate results at station X4, 50 m. were entered twice as 7·2 and 5·1, the same excess total iron figure, 17·3, being entered for both.

The results for station X5, 5 m. ('particulate $FePO_4$', 0, and excess total iron, 30 units) are anomalous and affect the average for the first group in the way shown. The inference is strong that the irregularities in the determinations of inorganic phosphate are in fact due to random occurrence of particulate ferric phosphate and that this particulate ferric phosphate is associated with the largest particles or least well-dispersed fraction of the particulate iron. The ferric phosphate was most probably included in faecal pellets (Cooper, 1948*b*).

TABLE IX. RELATION BETWEEN PARTICULATE $FePO_4$ DEDUCED FROM PHOSPHATE ANALYSES AND 'EXCESS TOTAL IRON'

(mg.-atom/m.^{3}) or (mg.-mol./m.^{3}) × 100

'Particulate $FePO_4$' range	No. of iron analyses	Excess total iron, average with standard deviation	
0–1·1	8 9	3·9 (excluding X5, 5 m.) 6·8 (including X5, 5 m.)	±3·8
2·0–3·8	8	13·0	±8·9
4·4–7·8	10	17·1	±8·6
8·6–11·8	4	27·7	±17·9

The assumption that the sample from each station giving the lowest analysis for phosphate contained no particulate $FePO_4$ is, in general, unlikely to be true. The estimates of the distribution of ferric phosphate at the Cruise X stations set out in Table X are therefore minimal.

TABLE X. MINIMAL PARTICULATE FERRIC PHOSPHATE CONTENT AT STATIONS ON CRUISE X

(mg.-mol./m.^{3} × 100)

Station ... Depth (m.)	X1	X2	X3	X4	X5	Mean
0	0	—	0	2·9	4	1·7
5	4	9, 0, 5, 0	1	2·0	0	2·1
25	6	7	4	6·4	1	4·9
50	0, 9	4, 0	3	7·2, 5·1	3, 2	3·6
70	12	9	1	—	—	5·7*
90	—	—	—	0·5, 0, 0·2	—	
95	—	—	—	—	1·1, 0·7	

* Excluding X4, 90 m.; see below.

Particulate ferric phosphate, like total iron, may possibly be greatest in bottom water. Similar but less clear-cut deductions may be drawn from other stations worked in January 1947.

For station X4 evidence has already been produced (p. 287) that the very low reducible and total iron in the bottom-most layer of water (90 m.) might be attributed to removal of particulate iron by bottom-dwelling animals, such as the suspension feeding mollusc, *Pinna*. At the time of analysis the low bottom phosphate, compared with samples from 25 and 50 m., was disconcerting, resulting in triplicate analyses of bottom water made 43, 44 and 62 hr. after collection. The very close agreement, 37·6, 37·1 and 37·3 units now suggests that *Pinna* had done their work well, leaving no particulate phosphate at all in the bottom water. Under the isothermal, isohaline conditions prevailing, 37·3 units appears to be a precise measure of the truly dissolved inorganic phosphate of the water column. If this premise may be accepted, the results for station X4 in Table X represent not the minimal but the actual distribution of particulate ferric phosphate, amounting at 50 m. to as much as 6 units (=0·06 mg.-mol./m.^{3} $FePO_4$).

Classification of the Forms of Iron in Sea Water

The forms of iron which may be present in sea water may be classified as follows:

A. *Uniformly dispersed iron*

(1) *Ionic iron.* Cationic iron, Fe^{++}, $FeOH^{++}$ and Fe^{+++} in true solution in sea water at equilibrium will amount to not more than 10^{-8} mg.-atom/m.^{3} (Cooper, 1937). Since equilibrium is only slowly attained, somewhat more may exist in sea water in which iron is in process of regeneration and redispersion. Ferrite anion, H_2FeO_3', may also perhaps be present in similar amount (Cooper, 1948*b*). Ionic iron is never likely to be detectable by chemical analysis.

(2) *Dissolved inorganic complexes.* Ferrifluoride is readily hydrolysable by sea water (Cooper, 1948*b*) and no evidence for any other inorganic complexes has yet been produced.

(3) *Dissolved crystalloidal or dispersed colloidal organic compounds.* Ferricitrate, when added to sea water, proves to be one of the less readily hydrolysed complexes of iron and there is indirect evidence of the existence of citrate in the sea. Crystalline calcium citrate tetrahydrate was dredged by R.R.S. *Discovery II* at station 417, 71° 22′ S., 16° 34′ W. in 2580 m. and appears quite definitely to have been formed *in situ* (Bannister & Hey, 1936). The bottom water of the Weddell Sea therefore contains sufficient citrate-ion to exceed the solubility product of calcium citrate. Ferricitrate may therefore exist in natural sea water. Breakdown products of haemoglobin and cytochrome such as haematin are also likely. Haemoglobin and haematin have both been found to be unusable as sources of iron by diatoms (Harvey, 1945, p. 35). The iron found in filtered deep ocean water by Rakestraw *et al.* (1936) and Thompson & Bremner (1935*b*) may well be attributable to organic iron which may or may not be directly assimilable by plants.

(4) *Colloidal inorganic compounds* such as ferric hydroxide or phosphate held in a dispersed sol by mucilaginous or other organic 'protective' colloids. Harvey (1937*b*) has shown that hydroxylic substances impart considerable protection to ferric hydroxide sols which often then become electronegative. Given time enough they all hydrolyse and ferric hydroxide precipitates.

B. *Aggregated or particulate iron*

(1) *Discrete flocculent particles of ferric hydroxide or phosphate.* There is good evidence for the existence of both in sea water (Harvey, 1937*a*, *b*).

(2) *A unimicellar film of ferric hydroxide*, electropositive and unprotected by organic colloids, covering a considerable part of the sea surface.

(3) *Ferric hydroxide or phosphate adsorbed* upon the surface of organic or inorganic detritus, upon living diatoms (Harvey, 1937*a*) or upon other phytoplankton.

(4) *Iron in faecal pellets.* The particulate ferric phosphate indicated by analysis is likely to be associated with, or to arise from, faecal pellets (see Cooper, 1948*b*). Since the gut of many marine animals is considerably more acid than sea water, iron and phosphate there meet under conditions well suited to the formation and precipitation of ferric phosphate. There also ferric hydroxide and phosphate will receive 'protection' from slime and mucilage. It remains to be seen what happens to iron when bacteria break down excreta, returning the more soluble components to the water.

These four fractions must together be mostly responsible for the 'coarsely particulate reducible' fraction amounting at midwinter to 0·19 ± (S.D.) 0·12 mg.-atom/m.^{3} in the 0 to 50 m. layers. In summer water at least, much of this particulate reducible iron is soluble at pH 4. Many of the particles must be large, 100 μ or more in diameter.

(5) *Organically bound iron* in the cells and tissues of living and dead plants and animals. With this fraction and perhaps with faecal pellets also may be identified the 'very coarsely particulate unreducible fraction' found in the bottom water, there amounting to about 0·32 ± (S.D.) 0·36 mg.-atom/m.^{3}. There must be some such iron in the upper waters also.

(6) *Terrigeneous iron* in clay and suspended mineral matter derived from the land. Such, in general, will not be determinable by the methods employed here though they will figure in analyses by the methods of T. G. Thompson and his collaborators.

Possible Lines of Advance

Assessment of the distribution of iron and of a plankton population by examination of small samples of water suffer from similar drawbacks. Only very large numbers of samples can overcome the great variability due to swarming or concentration in some places and not in others of plants, animals and their excretory products. Further analyses of sea water for iron by existing methods do not therefore offer the most promising line of advance.

Single particles—diatoms, faecal pellets, organic and inorganic detritus—need to be examined by microscopic and microchemical techniques to assess the nature of the particulate distribution of iron. The particles in the bottom layers and their interchange with the upper layers especially need attention. The adsorption and assimilation of iron by diatoms, centric and pennate, flagellates and other planktonic algae demands further knowledge. Do the plants gather all the available inorganic iron to themselves leaving none for later generations except that arising from their own death? Must forms of iron other than hydroxide and phosphate first be hydrolysed? What is the function of iron in auxospore formation and expansion? Are any organisms favoured by the concentration of iron and possibly ammonia (Cooper, 1948*a*) in the surface film? In what form is the iron in animal faeces and how quickly is this iron made available to plants? Again, do extensive beds of bottom-dwelling suspension feeders immobilize sufficient iron to affect the productivity of the overlying water?

SUMMARY

With 2:2′-dipyridyl as reagent for reducible and total iron, determinations were made on samples from the western English Channel at midwinter 1946–47, at the time of the maximum of phosphate, and also in July 1936.

The midwinter results have been treated statistically and the errors of analysis assessed.

Unlike phosphate and nitrate, much of the inorganic iron occurs as particles of fair size, distributed at random in the water. In winter there is no statistically significant difference between the total iron content of samples drawn from 0·5, 5, 25 and 50 m. depth, the grand mean and standard deviation for the whole area being 0·25 ± 0·11 mg.-atom/m.^{3}. The reducible iron for the same depth range and area was 0·19 ± 0·14 mg.-atom/m.^{3}. There appears to be about 0·06 mg.-atom/m.^{3} of iron which is reasonably highly dispersed and not determinable until the water has been oxidized with bromine.

In the bottom layers of water, although the reducible fraction differs little from the overlying layers, the total iron shows a very much greater mean value and variance.

The very low content of total and reducible iron and of particulate ferric phosphate in bottom water at a position 49° 30′ N., 5° 00′ W. has been provisionally attributed to removal by a dense bed of suspension feeders, possibly the mollusc *Pinna*.

By a statistical examination of the analytical results it has been deduced that the particulate fraction in the upper 50 m. was distributed on an average amongst about 45 particles per litre, each containing about 0·24 μg. Fe and with a diameter of about 160 μ. This result has been compared with data on the distribution of iron in plankton organisms.

As a statistical average waters richer in phosphate were also richer in total iron, the atomic ratio Fe/P being about 0·57.

In July 1936 the 'elegans' water to the westward was much richer in both phosphate and total iron than the more eastern mixed water containing *Sagitta setosa*. The results agree well with the conclusions drawn from the cruises at midwinter 1946–47.

In 1933–34 concentration of iron was frequently observed in the surface layers; in 1946–47 it was not. In the earlier work the surface film was always cut and included in the sample, in the later it was not. The probable amount of

a surface unimicellar film of electropositive unprotected ferric hydroxide has been calculated and agrees well with observation.

Particulate ferric phosphate was found to the extent of about 0·06 mg.-mols/m.^{3} This appears to increase towards the bottom.

The success of the work at Newlyn in January 1947 owes much to the willing co-operation of Capt. Creese and the crew of R.V. *Sabella* under very adverse weather conditions. To Mr P. G. Corbin grateful thanks are due for undertaking single-handed the supervision of all the scientific work at sea on stations never more than two hours apart for two or three days on end. The statistical development would not have been possible without the unstinted assistance of Mr G. M. Spooner.

APPENDIX I

STATISTICAL METHODS USED AND CORRECTION TERMS (SEE P. 281)

Two correction terms were needed, one for the extinction of light by the colour of ferrous-tris-dipyridyl formed from iron impurities in the reagents and determinable in freshly distilled water, the other for the turbidity or extinction due to scattering and absorption by substances dissolved or suspended in the sea-water samples. These were determined separately and the combined extinctions subtracted from the extinctions observed with the sea-water samples plus reagents. To measure each of these corrections at all accurately taxes the instrument and the observer, and in view of shortage of time four samples only from each cruise were examined for turbidity and the mean value applied as a correction to all analyses made on that cruise. The standard deviations of these mean values were actually less than the values reported on sub-samples of one sample. No error is therefore introduced into the statistical treatment. Later in the year with much more plankton variably distributed this procedure would not have been justified.

Finally in all work flasks, after all-night soaking with chromic cleaning mixture, were left for several hours with slightly acid tap water to leach away adsorbed contaminants from the glass. Flasks were covered with inverted crystallizing dishes except when an operation was in progress. Reagents were added from burettes which also were protected from dust by inverted test-tubes.

The large random variations in reducible and total iron discussed in the foregoing paper might reasonably be attributed to a defective method of analysis. That the method is sound for well-dispersed iron is shown by the following experiment. Samples from station E 1, 25 m. depth, were brought in on 27 February 1947 in Winchester bottles. Since no membrane filters were available, on 3 March part was filtered under suction through a Whatman No. 544 paper which is hardened, slow filtering and retentive, whilst part was left unfiltered. Several series of analyses were carried out in sextuplicate to justify evaluation of the variance and standard deviation. Parallel determinations were made on water drawn from the same station at 5 and 67 m. depth.

Series 1. On 5 March, 1 l. of filtered 25 m. water was acidified with 2·5 ml. 4 N-HCl. From this were measured six 150 ml. subsamples for determination of reducible iron.

Series 2. As series 1 but on 5 March 51 units Fe as ferric alum were added to the litre of water after filtration and *acidification.*

Series 3. As series 1 except that the sea water was unfiltered, the storage Winchesters merely being well shaken.

*Series E*1, *5 m., unfiltered* and *Series E*1, *67 m., unfiltered.* Exactly as Series 3.

Series reagent blank. Distilled water was treated precisely as Series 1 but in triplicate only. On each subsample, however, eight drum readings were made instead of four to give the same total number.

Unfiltered turbidity series. Unfiltered water from 25 m. was transferred from the storage Winchester, without treatment other than shaking, to the absorption tube for measurement of colour due to absorption and scattering by constituents of the water.

Filtered turbidity series. Filtered 25 m. water was similarly examined.

Upon all these subsamples, measurements of colour had to be made with the S 50 filter of the Pulfrich Photometer with the minimum of instrumental and personal bias. All were made on one day, 7 March. There is a slight backlash in the mounting of our Pulfrich eyepiece, spectral filters and drums so that a jolt is always liable to cause a small shift of zero. This source of error is guarded against by a control reading with distilled water (against the distilled water always present in the twin tube) every eighth or tenth determination. No such error arose in this experiment. More serious is the tendency of most observers more or less unconsciously to force subsequent readings on a sample to fall into line with the first. This human weakness is particularly hard to overcome with the highly subjective matching of colours. On 6 March therefore, the arbitrarily numbered flasks of all the above series were placed in random order with the further restriction that no two flasks of the same series were allowed to come next to one another. When colour comparison was made the following day, readings in quadruplicate were entered on a separate sheet in the order in which the flasks presented themselves. The two correction terms which have to be applied are set out in Table XI, where d is the deviation of the observed extinction from the mean. This extinction (E) is the product of an extinction coefficient and the length of the absorption tube in appropriate units, here 25 cm.

The higher turbidity and variance of the filtered compared with the unfiltered water requires comment. On 7 March large numbers of phytoplankton cells were observed in the absorption tubes containing filtered water. Similar cells were seen in the water in the last Winchester to be used but not in numbers in any of the other experimental flasks, whether the water had been filtered or not. On 3 March at the start of filtration the paper had not bedded down well in the Buchner funnel and consequently the faulty filtrate was filtered again. Evidently a few cells were left in the filtration flask and were transferred to the first Winchester to be filled and the last to be emptied. There in the next 4 days they must have found conditions favourable for rapid division which were absent in the remaining two Winchesters of filtered water and experimental flasks. Though these Winchesters were for part of their time in a cupboard, sufficient attention was not given to keeping them away from light. The Winchesters of unfiltered water were never removed from their cupboard except when required. The explanation of the very high variance is clear. Since the errant Winchester was supposed to contain homogeneous water it was not shaken very thoroughly before transferring the subsamples to flasks, which therefore, in fact, contained varying amounts of the cell culture causing varying extinction of light to be measured. Unfortunately at the time, the possible significance of the observation for work on cultures was not appreciated so that the species responsible was not identified. None of the other series of measurements with filtered water contained water from this Winchester.

TABLE XI. EXTINCTIONS REQUIRED AS CORRECTION TERMS

$(E=\log_{10}I_0/I)$

Series	No. of sub-samples n	Arithmetic mean	Average deviation $\frac{\Sigma d}{n}$	Variance $\times 10^6$*	Standard deviation $\sqrt{\frac{\Sigma d^2}{n-1}}$
Reagent blank in dist. water	3	0·0106	0·0005	0·39	0·00062
Turbidity, unfiltered water	6	0·0288	0·0008	0·97	0·00098
Turbidity, filtered water	5	0·0318	0·0018	51·90	0·0071

* This and Table XII are the only ones where variance has to be multiplied by 10^6; in all others the units have been chosen to avoid this operation.

In consequence of this, the rather lower and more regular turbidity determination on the unfiltered water has been applied as the correction term for all samples. The accuracy but not the precision of these iron analyses may therefore have been slightly affected. However, this experiment was concerned more with precision than with absolute accuracy. The correction term to be subtracted from the iron determinations is therefore the sum of the first two extinctions in Table XI:

$$0{\cdot}0106+0{\cdot}0288 \pm 10^{-3}\times\sqrt{(0{\cdot}39+0{\cdot}97)}=0{\cdot}0394 \pm 0{\cdot}00117.$$

The variance was $1{\cdot}357\times10^{-6}$.

The extinctions for the series made to determine reducible iron in filtered or unfiltered sea water are set out in Table XII.

TABLE XII. EXTINCTIONS FOR REDUCIBLE IRON IN THE SEA WATER SERIES

Series	No. of sub-samples	Arithmetic mean	Average deviation	Variance × 10⁶	Standard deviation
E 1, 25 m.					
1	5	0·0012	0·0051	40·04	0·00633
2	5	0·1061	0·0027	14·398	0·00379
3	6	0·0289	0·0141	365·48	0·0191
E 1, 5 m.	4	0·0152	0·0044	37·66	0·00614
E 1, 67 m.	4	0·0238	0·0051	50·61	0·00711

The difference between series 1 and 2 showed that an addition of 51 units Fe to acidified sea water gave an increment of extinction amounting to 0·1049 ± 0·0074. The standard deviation is twelve times that in distilled water and is equivalent to 3·8 units Fe. This factor has been used for computing the contents of reducible iron set out in Table XIII.

TABLE XIII. REDUCIBLE IRON IN WATER COLLECTED 27. ii. 47

(mg.-atom/m.^{3} × 100)

Series	Abbreviated description	Reducible iron with standard deviation
E 1, 25 m.		
1	Filtered, no added iron	0·6 ± 3·08
2	Filtered and acidified before addition of iron (510 μg.-atom)	51·6 ± 1·84
3	Unfiltered, no added iron	14·1 ± 9·29
E 1, 5 m.	Unfiltered, no added iron	7·4 ± 2·98
E 1, 67 m.	Unfiltered, no added iron	11·6 ± 3·46
Integral mean for reducible iron at E 1, 27. ii. 47		11·5

Within the limit of error of the method, filtration through Whatman No. 544 filter paper removed all the reducible iron in the water. Providing that the sea water is acidified before the addition of ferric salt the increment in colour is identical with that in distilled water (unpublished work). There is no 'salt error'. Unfiltered sea water from 25 m. therefore contained 14·1 units reducible iron, all of which was removable by filtration, whilst at 5 and 67 m. there was somewhat less. Again, the standard deviation on filtered water attributable to analytical error amounted to 3·1 units.

Except in considering particle size (pp. 288–91), no assumption has been made as to the mathematical nature of the statistical distribution other than that variance is an additive property. Clancey (1947) has concluded that many of the distributions met in chemical analysis depart radically from the 'normal' and are possibly to be regarded more correctly as forms of 'rare occurrence' distributions. These have to be combined with distributions, probably of the 'normal' or Poisson type, arising from the interplay of biological and chemical factors in the water.

APPENDIX II

STATISTICAL ANALYSIS OF THE ‘TOTAL IRON’ DATA, 1946–47, BY G. M. SPOONER, M.A.

The ‘total iron’ data presented in Table II have been arranged so that the values for each depth at different stations are grouped; except for the deepest sample at each station, taken less than 20 m. from the bottom. Such samples are separated out as ‘bottom’ samples.

When this is done it is at once apparent—as indeed is evident from inspection of Table II—that the bottom readings are more variable than those taken well away from the bottom (‘upper water layers’) and include most of the higher values. By contrast, depths from 0 to 50 m. give more uniform results, both separately and when compared with each other. It is also clear that one station, A3, which had been worked in rough weather, stands apart from the rest, and evidently presents some anomaly: it is excluded from the computations which follow.

The means and variances for the values obtained at different depths are given in Table XIV.

TABLE XIV. TOTAL IRON AT DIFFERENT DEPTHS

Depth (m.)	No. of analyses	Mean ±S.E.	Sum of squares	Degrees of freedom	Mean square (variance estimate)	S.D. ±S.E.
Upper water layers (0–50 m.):						
0	8	23·13±2·83	448·9	7	64·13	8·01±2·00
5	19	24·84±2·55	2098·5	18	116·59	10·80±1·75
25	22	25·64±2·66	3275·1	21	155·96	12·49±1·89
50	19	25·79±2·24	1713·2	18	95·18	9·76±1·58
Total	**68**	**25·16±1·316**	**7535·65**	**64**	**117·74**	**10·851±0·9305**
Intermediate water (60–75 m. below the surface and 23–37 m. above the sea bed):						
	8	45·6 ±6·07	2059·9	7	294·27	17·15±4·29
Bottom water:						
	23	50·87±8·03	32,573·6	22	1480·62	38·48±5·68

The following points deserve notice:

(1) The mean value for total iron at the bottom is larger than that in the upper layers. Though the estimate for the bottom is not very precise, it can be said to be roughly twice as great. (2) The variation between analyses at one depth is clearly greater on the bottom, the standard deviation being some 3 to 4·5 times that of analyses from the upper layers. (3) Within the ‘upper water layers’, analyses from different depths (0, 5, 25, 50 m.) do not show any marked differences, either in mean values, which indeed seem more uniform than might have been expected, or in variation between analyses. This phenomenon will be examined more closely below, but in the meantime it is

useful to call attention to the values for the total number (68) of analyses for the upper water layers, which are given in heavier type in Table XIV. (4) The few analyses from depths greater than 50 m., but not close to the bottom, here classed as 'intermediate' depths, clearly give results of an intermediate character—that is, intermediate between those from the shallower depths (considered separately or combined) and the bottom.

The figures suggest that close to the bottom there is rather more iron than in the main part of the water column, and that it is more erratically distributed—presumably because part of it there occurs in coarse particulate aggregations which are normally absent from the upper layers. The influence of the bottom is felt some little distance above, but for the area under survey, where depths ranged from 80 to 120 m., it can be said that the top 50 m. at least was free from this influence. Throughout this top 50 m. conditions appear to be comparable.

Attention will now be confined to the 68 analyses from the top 50 m. (Fig. 2, upper part of middle histogram less readings for station A3), and the variation found amongst them examined in greater detail. These 68 analyses, with a mean of 25·16 units, have a 'Sum of Squares' of 7583·2, giving (for 67 degrees of freedom) a mean square of 113·18 and S.D. of 10·64 (see foot of page). The latter is relatively high, and indicates that 5% of the analyses may be expected to lie outside the (approximate) limits of 4 to 47 units. How much of this variation, it must be asked, is due to differences between the several stations at which samples were taken, or to differences between depths? And how far has it been reduced by triplicating the analyses of some of the samples? To attempt an answer, 'analysis of variance' technique must be used.

At the outset it is evident that difficulties may arise through the lack of symmetry of the original data. As has been pointed out (p. 280), circumstances prevented measurements at all depths at every station, while it proved possible to replicate some of the samples, but by no means all. It is thus necessary to proceed with caution in attempting a partition of the variance, and to guard against any bias which might lead to invalid conclusions. As will be seen, however, difficulties largely resolve themselves, owing to the high degree of homogeneity which the data possess. The main object is to arrive at an estimate of the sampling variance when the effects of any differences between depths or between stations have been excluded.

The figures in Table XIV have already indicated that depths down to 50 m. give comparable results. Analysis of the variance shows:

	Degrees of freedom	Sum of squares	Mean square
Between depths	3	47·57	15·9
Within depths*	64	7535·65	117·74
Total	67	7583·2	113·18

* Sum of the separate items given in Table XIV.

Depth difference has therefore introduced no extra variation, since the value 117·8 is not less than 113·18. Indeed the effect shown is all the other way, though for only 3 degrees of freedom the value 15·9 is not quite significantly low even in a strictly orthogonal comparison. By chance the readings from the four depths average out more closely than might have been expected. The result gives a wide margin for any small bias which the lack of symmetry of the data as a whole may have introduced.

We can therefore in full confidence disregard differences in depth, when considering the upper layers. This fact is most fortunate, as the original data can now be re-arranged ignoring depth, and much of the asymmetry disappears. The main irregularity now lies in the distribution of replicate readings. These, however, gave a consistent form of result whenever they were made, and they can be safely regarded as representative of the whole sample. (An analysis of the samples with which they are concerned is given below.) Analysis may now proceed to separate off the influences of station-diversity and replicate sampling, as follows:

	Degrees of freedom	Sum of squares	Mean square (variance)	S.D.
Between stations	16	3933·2	247·8	
Between subsamples	17	1101·7	64·8	8·05 (±1·34)
Between samples (within stations)	34	2548·4	74·95	
Total	67	7583·2	113·18	10·64 (±0·913)

The higher variance for the 'between stations' component is significantly different from the other two, and indicates, not surprisingly, that the variability of the analyses has been somewhat increased by taking samples from different places. (Diversity between stations is mainly due to the low-value stations A4 and A6 and the high-value station X3: there seems to be little difference between the majority of the stations.)

The variance between the subsamples of those samples for which there are replicate analyses (64·8 sq.units) is lower than the other components, though very little less than that of the residual variance (74·95 sq.units), thus emphasizing the relative uniformity of the distribution of iron at any given station.

Note. The eight samples for which there is more than one analysis, and which therefore are involved in the 'subsample' data, happen to be quite uniform among themselves, though four different stations are represented. Analysis gives:

	Degrees of freedom	Sum of squares	Mean square	S.D.
Between subsamples	17	1101·7	64·8	8·05
Between samples	7	275·3	39·3	6·27
Total	24	1377·0	57·4	7·57

(The data include twenty-five analyses, made up of three each from samples A 1, 5 m.; A 1, 25 m.; A 7, 5 m.; A 7, 25 m.; C 4, 50 m.; X 4, 25 m.; X 4, 50 m.; and four from X 4, 5 m.).

By eliminating the effects due to the multiplicity of stations and to the occasional subsampling, the variance of 'total iron' analyses is reduced from the first over-all estimate of 113·18 ($=10{\cdot}64^2$) to 74·95 ($=8{\cdot}66^2$). This represents a value for the variance which might be found between a number of analyses from the same water-column (down to 50 m.) at any one station. If the analyses are confined to *one position* in the water-column, i.e. become replicates of a single sample in the sense employed here, the value for the variance will almost necessarily be less than 74·95, though not necessarily much less. Our direct and independent estimate of this value is 64·8, the significance of which is thus enhanced.

The 'refined' variance value of 64·8 is important, as it is a measure of the variation which remains between samples which should duplicate each other, and should be virtually identical in chemical composition. It is much larger than any possible variance resulting from errors introduced during the procedure of chemical analysis (see Appendix I). The conclusion reached therefore is that *even in the upper water layers the iron is distributed in particulate form*. The size of the particles, though less than that of the coarse particles which seem to occur on the bottom (p. 286), must be such that there is quite a small average number in a volume of 150 c.c., and random variations from that number can produce considerable differences in total iron between adjacent bodies of that volume.

From the actual derived value for the variance (64·8), the possibility is open for estimating this degree of aggregation of the iron, i.e. of the size and density of the particles with which it is associated, once allowance has been made for the error inherent in the chemical technique used in handling the samples in the laboratory.

APPENDIX III

Statistical Analysis of the 'Reducible Iron' Data, 1946–47

The data for reducible iron have been examined (Table XV) by the method used for total iron by Mr Spooner in Appendix II. The number of analyses is considerably less and the conclusions are to that extent less certain. The result at X1, 75 m. depth (79 units) is omitted.

(1) The results at 5, 25 and 50 m. are uniform, indeed more so than might have been expected. There are only three surface (0·5 m.) results and these are all relatively high (27, 20 and 53 units). These, standing by themselves, have little significance and there is no good reason for leaving them out of the further statistical analysis. This leads to a mean reducible iron content of the upper layers (0·5, 5, 25 and 50 m.) of 19·3 units.

(2) The mean reducible iron content of the bottom waters was less than in the upper layers though probably not significantly so. The result is in strong contrast with that for total iron.

(3) The variance and standard deviation was much the same in bottom water as in the upper layers. The number of analyses scarcely justifies a further analysis on the lines of that for total iron.

(4) The difference between the mean values for total and for reducible iron gives a measure of the unreducible fraction which has been worked out for the several standard depths other than the surface (Table XVI). The variance estimate, also found by difference, is sometimes negative. For the upper layers (5, 25 and 50 m.), the unreducible iron amounts to about 6 units. The ratios of the variances of total and of reducible iron examined in terms of their degrees of freedom suggests that the variance estimate of the unreducible iron does not differ significantly from zero. It is safe to say that the variance estimate of the unreducible iron is negligible or at least quite small compared with that of reducible iron in the upper layers. This fraction (about 6 units) is therefore reasonably uniformly distributed throughout the upper layers. At midwinter with vertical mixing of the water proceeding freely this must be true of the bottom water also. Also the random distribution of total iron in the upper layers is entirely due to the reducible component, i.e. ferric hydroxide

TABLE XV. REDUCIBLE IRON AT DIFFERENT DEPTHS

Depth (m.)	No. of analyses	Mean ± S.E.	Sum of squares	Degrees of freedom	Mean square (= variance estimate)	S.D. ± S.E.
Upper water layers (0–50 m.):						
0	3	33·33 ± 10·56	607	2	303·5	17·39 ± 7·48
5	8	17·88 ± 2·28	291	7	41·6	6·45 ± 1·61
25	11	16·36 ± 4·50	2228	10	222·8	14·92 ± 3·18
50	9	19·55 ± 4·37	1377	8	172·4	13·02 ± 3·09
Total	31	19·32 ± 2·49	5193	27	192·3	13·87 ± 1·76
Intermediate water:						
	4	13·75 ± 4·28	220	3	73·3	8·56 ± 3·02
Bottom water:						
	8	12·75 ± 4·81	1302	7	186·0	13·64 ± 3·40

TABLE XVI. UNREDUCIBLE IRON AT DIFFERENT DEPTHS AS DIFFERENCE BETWEEN MEANS FOR TOTAL AND REDUCIBLE IRON

Depth (m.)	Difference of means	Difference of mean squares (= variance estimate)
Upper water layers (0–50 m.):		
5	6·96	+75·0
25	9·28	−66·8
50	6·24	−77·2
Total	5·84	−74·6
Intermediate water:	31·8	+221·0
Bottom water:	38·1	+1295

and phosphate. (These deductions assume that there is no inverse correlation between reducible and unreducible iron. Only further investigation can rule out this unlikely event.)

TABLE XVII. STATISTICAL ANALYSIS OF THE IRON CONTENT OF BOTTOM WATER

Fraction	No. of analyses	Mean	Variance estimate	Standard deviation
Total iron	23	50·87	1480·62	38·48
Reducible iron	8	12·75	186·0	13·64
Dispersed unreducible iron	—	6	Approx. zero	Approx. zero
Particulate unreducible iron	—	32·1	1294·6	36·0

It will be seen from Table XVII that when the reducible and dispersed unreducible fractions are separated from the total iron in bottom water, that a very large particulate unreducible fraction is left—32 units with the very large standard deviation of 36.

A similar examination of the results for the intermediate layer (Table XVIII) gives positive but rather lower values of the mean and standard deviation.

TABLE XVIII. STATISTICAL ANALYSIS OF THE IRON CONTENT OF INTERMEDIATE WATER

Fraction	No. of analyses	Mean	Variance estimate	Standard deviation
Total iron	8	45·6	294·27	17·15
Reducible iron	4	13·75	73·3	8·36
Dispersed unreducible iron	—	6	Approx. zero	Approx. zero
Particulate unreducible iron	—	25·85	221·0	14·9

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SOME CHEMICAL CONSIDERATIONS ON THE DISTRIBUTION OF IRON IN THE SEA

By L. H. N. Cooper, D.Sc., F.R.I.C.

Chemist at the Plymouth Laboratory

Three purely chemical topics which have arisen in the course of the investigation described in the preceding paper (Cooper, 1948) will be discussed; first, a theoretical treatment of the formation and stability of ferric phosphate in sea water; secondly, an explanation as to how 2:2′-dipyridyl may react with ferric iron at high dilutions in natural waters to give the red ferrous complex; and thirdly, a short account of an experiment which showed ferrifluoride to be unstable in sea water.

Formation and Stability of Ferric Phosphate in Sea Water

Two series of experiments in this laboratory by Harvey (1937) and by the writer (unpublished) on the precipitation of iron from sea water containing phosphate and hydroxyl ions (pH 8·1) do not agree. Sometimes much of the phosphate is precipitated, sometimes none. Much closer control is necessary but it has not been clear what form this should take. The following theoretical examination, imperfect though it is, may help in the design of such control.

Pugh & du Toit (1936) examined the ionic exchange or hydrolysis of ferric phosphate and silicate in relatively concentrated systems. Solutions of ferric chloride were titrated with solutions of phosphate or silicate containing varying amounts of sodium hydroxide. A ferric phosphate with a higher PO_4/Fe_2O_3 mol-ratio than 0·71 could not be prepared since compounds richer in phosphate hydrolysed until this ratio was reached. There is an optimum value of pH above which the ferric phosphate hydrolyses further with increasing hydroxyl-ion concentration. The same is true of ferric silicate. At pH 8·0 and above, in presence of hydroxyl, silicate and phosphate in solution, ferric hydroxide would be the stable solid phase. The isoelectric point of ferric hydroxide prepared from its chloride is said to be pH 7·1 so that at pH 8·1 ferric hydroxide should be regarded rather as the very sparingly soluble ferrous acid, H_3FeO_3, which may be expected to dissociate

$$H_3FeO_3 \rightleftharpoons H^+ + H_2FeO_3'.$$

Since $FeOH^{++}$ is the dominant ferric cation at the isoelectric point, for electroneutrality of the micelle, the concentration of its anion, H_2FeO_3', should be twice that of its cation, $FeOH^{++}$. This (Cooper, 1937*b*, equation 12) will be about $10^{-12\cdot54}$ at 18° C. The solubility product of ferrous acid, $(H^+)(H_2FeO_3')$ will therefore be of the order

$$10^{-7\cdot1} \times 12 \times 10^{-12\cdot54} = 10^{-19\cdot3}.$$

At pH 8·1 the molar concentration of the ferrite ion would be about $10^{-11\cdot 2}$ or 0·006 μg.-atom/m.^{3}. This figure cannot be very accurate since the isoelectric point of ferric hydroxide sols depends greatly upon the method of preparation.

Revut (1936) also states that on standing ferric phosphate sols slowly hydrolyse. The complexes may vary much in structure and calcium phosphate may be included (Kheifetz, 1936).

In the sea ferric hydroxide and phosphate will almost always be colloidal, conceivably but very rarely micro-crystalline and never macro-crystalline. In an azoic world, given sufficient time, thermodynamic equilibrium would no doubt in the end be reached, whereas in temperate surface waters of the sea, the speed of the life cycle is likely never to allow equilibrium conditions to be even remotely approached. Equilibrium values for ferric hydroxide have been discussed (Cooper, 1937*b*) and at *p*OH 6·5 (pH 8 at 10° C.) (Cooper 1937*a*) we should expect $10^{-10\cdot 9}$ μg.-atom/m.^{3} Fe^{+++}, $10^{-5\cdot 3}$ μg.-atom/m.^{3} $FeOH^{++}$ and possibly 10^{-3} μg.-atom/m.^{3} H_2FeO_3'.

The amount of undissociated phosphoric acid, H_3PO_4, present in sea water must be minute (Nims, 1934). Phosphate occurs mostly as the ions, H_2PO_4' and HPO_4''. The second dissociation constant in terms of activities at infinite dilution has been most carefully determined by Nims (1933):

$$K_2 = \frac{a_{\mathrm{H}}\, a_{\mathrm{HPO_4}}}{a_{\mathrm{H_2PO_4}}} = 5{\cdot}98 \times 10^{-8} \text{ at } 18^\circ \text{ C.} \qquad (1)$$

At finite concentrations of solute, activity coefficients have to be introduced. Extrapolation from Nims' experimental upper limit of ionic strength, 0·15, to the ionic strength of sea water, 0·7, would involve laborious computations which the problem does not at present justify. Nevertheless, to give shape to the problem, the concentration of the tribasic ion, PO_4''' will be calculated at pH 8·0 and 8·3 in a solution 'at infinite dilution', assuming that activity coefficients are all unity and that activities may be equated to molarities, written within parentheses. Since the concentrations of H_3PO_4 and PO_4''' are negligible compared with H_2PO_4' and HPO_4'', the total concentration, of dissolved inorganic phosphate, ΣP may be written

$$\begin{aligned} \Sigma P = (H_2PO_4') + (HPO_4'') &= \frac{(H^+)\,(HPO_4'')}{K_2} + (HPO_4'') \\ &= \left[1 + \frac{(H^+)}{K_2}\right](HPO_4''). \qquad (2) \end{aligned}$$

For the third dissociation constant,

$$K_3 = \frac{(H^+)\,(PO_4''')}{(HPO_4'')}, \qquad (3)$$

the literature values are divergent, Abbott & Bray (1909) giving $3{\cdot}6 \times 10^{-13}$ and Blanc (1920) 2×10^{-12}. A round figure of 10^{-12} will be assumed. Combining equations (2) and (3), we have:

$$(\mathrm{PO}_4''') = \frac{K_2 K_3}{(\mathrm{H}^+)\,[K_2 + (\mathrm{H}^+)]}\,\Sigma P = Q \Sigma P. \tag{4}$$

At pH 8·0, $Q = 0{\cdot}86 \times 10^{-4}$,

and at pH 8·3, $Q = 1{\cdot}84 \times 10^{-4}$.

That is, if the alkalinity of sea water be raised from pH 8·0 to pH 8·3, the amount of tribasic ion 'at infinite dilution' would be doubled. In sea water the apparent dissociation constants will certainly differ markedly from those quoted, but the relative values of Q will be much less in error.

Now let us consider the partition of iron between hydroxide and phosphate in sea water. Sea water is sufficiently well buffered for the hydroxyl-ion concentration to be considered constant. By contrast the total concentration of phosphate ions, ΣP, is very low and not much greater than the amount of particulate ferric phosphate inferred from analysis (Cooper, 1948).

Let us *assume* that the solubility product of ferric phosphate,

$$K_{\mathrm{FePO}_4} = (\mathrm{Fe}^{+++})\,(\mathrm{PO}_4''') = 10^{-31{\cdot}5}. \tag{5}$$

The equilibrium concentrations of ferric ion (Cooper, 1937*b*) would be $10^{-19{\cdot}9}$ at pH 8·0 and $10^{-21{\cdot}3}$ at pH 8·3.

By combining equations (4) and (5):

$$(\mathrm{Fe}^{+++})\, Q \Sigma P = 10^{-31{\cdot}5},$$

so that at pH 8·0, $\Sigma P = 34$ and at pH 8·3, $\Sigma P = 110$ μg.-atom/m.^{3}.

This theoretical approach confirms the experimental finding of Pugh & du Toit (above) in relatively very concentrated solution that the hydrolysis of ferric phosphate becomes greater the more alkaline the water. The conditions least favourable to the stability of ferric phosphate must therefore arise in the upper layers of the sea, during active plant growth. The formation and stability of ferric phosphate is likely to be most favoured under the more acid conditions found in the gut of many animals. Ferric phosphate is likely therefore to be introduced into sea water in faeces. It should be stressed that only the relative and not the absolute magnitudes of these calculations have meaning since the solubility product of ferric phosphate, $10^{-31{\cdot}5}$, was arbitrarily selected to give an answer within the realm of experience.

Doubt as to the correctness of these deductions springs less from the rather arbitrary nature of the calculation than from our complete ignorance as to how rapidly equilibrium conditions are attained. In all experimental work involving ferric phosphate in sea water, the need is indicated for very accurate control of hydroxyl-ion concentration (strictly activity) and for attention to the time factor and to the physical condition of the precipitated phase. The topic merits study not only from a biological but from a geochemical point of view. The equilibrium between ferric, hydroxyl and phosphate ions would seem to be precariously balanced and not always rapidly attained. It is likely to be strongly displaced by hydrostatic pressure which will affect the co-precipitation of iron and phosphate in deep-water deposits.

Ferrous Iron in the Sea and in Lakes

2:2′-Dipyridyl is now often used for characterizing ferrous as opposed to ferric iron at high dilutions in lake water (e.g. cf. Mortimer, 1941). Determinations made in the English Channel by the writer in 1933–34 (Cooper, 1935, p. 422) and attributed to ferrous iron now appear to be nothing of the sort. An explanation is due. In the earlier work 100 ml. samples of sea water were treated with two drops of 4 N-HCl and 1 ml. 1% dipyridyl in 0·2 N-HCl. Harvey (1937) has shown, and the writer has confirmed, that at high dilutions ferric iron will give rise to the red ferrous-*tris*-dipyridyl complex.

In sea water particulate and colloidal ferric hydroxide, phosphate and the like will approach an equilibrium with Fe^{+++} and $FeOH^{++}$ whose concentration at the analytical pH of about 4·5 will not exceed about 50 μg.-atom/m.^{3}:

$$Fe(OH)_3 \rightleftharpoons FeOH^{++} + 2OH' \rightleftharpoons Fe^{+++} + 3OH', \qquad (1)$$

$$FePO_4 + 2H_2O \rightleftharpoons Fe^{+++} + H_2PO_4' + 2OH'. \qquad (2)$$

These ferric ions will seek an equilibrium with ferrous ions which will be governed by the poise and pH of the system

$$Fe^{+++} + e \rightleftharpoons Fe^{++}, \qquad (3)$$

$$FeOH^{++} + H^+ + e \rightleftharpoons Fe^{++} + H_2O. \qquad (4)$$

When undissociated dipyridyl (dipy) is present the ferrous ions will be rapidly removed.

$$Fe^{++} + 3\ \text{dipy} \rightleftharpoons Fe(\text{dipy})_3^{++}.$$

Reactions (1) to (4) will then proceed to restore the ferrous-ion concentration, providing that the necessary reducing electron can be found. If the oxygen electrode system, considered as a thermodynamically reversible system, be examined as the source of the electron:

$$O_2 + 2H_2O + 4e \rightleftharpoons 4OH',$$

we find that reduction of 200 μg.-atom/m.^{3} of ferric ion to ferrous ion would result in the oxidation of hydroxyl ion to 0·006 ml./l. dissolved oxygen. The change of poise of the system would be negligible as would the change in pOH or pH of even a weakly buffered water.

The reaction may also be formulated as proceeding through the weakly blue ferric-dipyridyl complex:

$$Fe^{+++} + 3\ \text{dipy} \rightleftharpoons Fe(\text{dipy})_3^{+++},$$

$$Fe(\text{dipy})_3^{+++} + e \rightleftharpoons Fe(\text{dipy})_3^{++}.$$

The redox potential of this last reaction exceeds unity.

The source of the reducing electron should not be ascribed solely to the hydroxyl ion-oxygen system which, in fact, is not thermodynamically reversible but rather to the poising system of the water considered as a whole. The point of the argument is to show that in presence of a powerful combining reagent for ferrous ion such as 2:2′-dipyridyl, ferric iron in a natural water at high dilution may seem to combine directly to give the ferrous-dipyridyl complex without needing the presence of a definite reducing agent in the usual macrochemical sense of the phrase. Thus the results in 1933 and 1934 reported as ferrous iron certainly included some ferric iron as well.

FERRIFLUORIDE IN SEA WATER

It was earlier suggested (Thompson, Bremner & Jamieson, 1932; Cooper, 1935) that ferrifluoride may play a part in the iron cycle in the sea. An experiment made in May 1936 now shows this to be unlikely.

A well-washed, freshly prepared precipitate of ferric hydroxide was redissolved by treatment with excess hydrofluoric acid in a platinum dish. Addition of an equivalent solution of sodium carbonate gave a white precipitate of sodium ferrifluoride which was well washed by decantation to remove excess hydrofluoric acid. A few crystals of the moist precipitate on a loop of platinum wire were added to 250 ml. of sea water. The suspension slowly became yellow and finally ferric hydroxide separated. This experiment was repeated several times and indicates that, due to one of the reactions:

$$FeF_6''' + 3H_2O \rightarrow Fe(OH)_3 + 3HF + 3F'$$

or

$$FeF_6''' + Al^{+++} + 3H_2O \rightarrow AlF_6''' + Fe(OH)_3 + 3H^+$$

ferrifluoride in sea water is unstable and plays no part in the iron economy of the sea.

SUMMARY

A theoretical study of the behaviour of ferric phosphate in sea water has been made with existing data. The conditions least favourable for the continued existence of ferric phosphate should occur in the upper layers of the sea during active plant growth. The formation and stability of ferric phosphate is likely to be most favoured under the more acid conditions found in the gut of many animals. Ferric phosphate is likely to be introduced into sea water in animal faeces. Experimental confirmation of this deduction is essential.

In all experimental work involving ferric phosphate in sea water, the need is indicated for very accurate control of hydroxyl-ion activity and probably pressure, and for attention to the time factor and to the physical condition of the precipitated phase. The topic is of geochemical as well as of biological interest.

Dipyridyl is a reagent for ferrous iron. Reasons are set out why in sea and lake water at high dilutions it may also determine ferric iron without presence of an added reducing agent.

Evidence is presented that ferrifluoride plays no part in the iron cycle in he sea.

ADDENDUM

The Editor has shown me the proofs of a contribution to this Volume (pp. 360–79) by S. M. Marshall & A. P. Orr (1948) on the effect of different plant nutrients upon the phytoplankton in Loch Craiglin. The deepest water (4–5 m.) was frequently oxygen-free, contained sulphide, and much resembled the freshwater studied by Mortimer (1941) in Esthwaite Water (English Lake District). Such a stratification is likely to lead to the following distribution of iron and phosphate.

Oxygenated upper layers. Any iron present is likely to be largely colloidal or particulate ferric hydroxide which may or may not combine with phosphate to give particulate ferric phosphate. The balance of evidence has suggested that normal sea water may be too alkaline for this to happen. In Loch Craiglin the pH of surface water may even rise to over 9.

Sulphide containing bottom water. In distilled water precipitated ferrous sulphide has a solubility of 70 mg.-mol/m.^{3} (Weigel, *cit.* Seidell, 1920, p. 345). Its solubility in sea water is likely to have the same order of magnitude. Consequently, any amount of iron likely to be present in the foul bottom water of Loch Craiglin could be retained in solution as dissolved ferrous sulphide. The flagellate, *Euglena proxima*, was present mostly in or near the boundary between the two layers.

On 1 August 1944 the loch had been fertilized with large quantities of superphosphate and sodium nitrate, most of which had been removed from the water by 7 August (Orr, 1947). Dissolved oxygen at 2 m. had risen to 292% 'saturated' and the pH to 9·82. On samples taken on 9 August Mr H. Barnes made some iron analyses by the method used at Plymouth and in the oxygen-rich, very alkaline water at 0, 1 and 2 m. was able to detect no iron. By contrast in the sulphide-containing water at 3 m. about 0·36 mg.-atom/m.^{3} ferrous iron was found. The criticism, made above, as to the soundness of analyses for ferrous iron by this method are not valid for reducing waters such as that at 3 m.

Iron, when once it has been immobilized in the bottom in any insoluble form, may be returned to the water physically by turbulence, by the agency of certain classes of animals, or by both together. Bacteria alone cannot bring it about under aerobic conditions. The important part played by faecal pellets in the bottom muds of the Clyde Sea area has been well shown by Moore (1931). The writer is being led more and more towards the view that detritus and suspension feeding animals hold a key position in the return of iron into circulation in a form usable by plants. It is surmised that these, either by triturating their food or by dissolving it in acid digestive juices, disperse iron surplus to their needs in their faeces and give it a measure of 'protection' by embedding it in organic colloids. After excretion into the overlying water, bacterial breakdown would further disperse this protected iron into a form usable by plants. This is a development of the argument already put forward by Harvey (1945, p. 137) as to the part played by zooplankton in the upper layers of the sea.

Though the minimal requirements of diatoms for iron are much less than those for phosphorus (Harvey, 1937), some iron in a usable form is essential. It would now seem likely that the planktonic plants over the continental shelf require a proper balance of animals, both planktonic and bottom dwelling, to maintain their supply of iron in such a usable form. If therefore after addition of phosphatic and nitrogenous fertilizers, the plant population should become so great as to exclude a balanced growth of animals then the circulation of iron in a usable form would cease completely. Unlike phosphorus and nitrogen, bacterial decay alone would be unable to redress the balance. Subsequent addition of further phosphate and combined nitrogen to an enclosed body of water would then cause little further production of phytoplankton. Something of this sort may have happened on occasion in Loch Craiglin though it is not possible to separate the effects due to possible lack of usable iron from those due to high pH and disturbance of the carbon dioxide-bicarbonate system.

I am much indebted to Dr A. P. Orr for allowing me to see the typescript of his paper which is to appear in the Proceedings of the Royal Society of Edinburgh, for a criticism of this addendum and for a statement of his views. It is only fair to add that the Millport work was carried out during the war years concurrently with other work of higher priority. Many factors, including those discussed here, were well appreciated but in the very limited time available could not be examined. It is surprising indeed how much valuable data he and Dr Marshall were able to collect.

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PARTICULATE AMMONIA IN SEA WATER

By L. H. N. Cooper, D.Sc., F.R.I.C.

Chemist at the Plymouth Laboratory

In the English Channel during the winter months vertical mixing is thorough, so that in 50–100 m. of water temperature and salinity are usually uniform from surface to bottom. Other truly dissolved substances would also be expected to be uniformly distributed. The erratic distribution of iron has been shown to arise from its particulate nature, whilst small vertical variations of inorganic phosphate in winter as well as occasional poor agreement between replicate phosphate analyses are most probably due to particulate ferric phosphate (Cooper, 1948).

Two features of the ammonia analyses made in 1930–31 have always caused the writer concern. That ammonia, with its ready solubility and inability to form insoluble compounds, must be in true solution seems axiomatic. Yet, on the three cruises to International Hydrographic Station E1 (72 m. depth) on 4 December 1930, 13 January and 4 February 1931, there were marked maxima of ammonia at surface and bottom (Cooper, 1933, fig. 6). Rapid though regeneration of ammonia from decaying material may have been, it is odd that vertical mixing could have allowed dissolved ammonia so to accumulate. Surface samples were taken with a wooden bucket and so included a portion of the surface film.

Wattenberg's absorptiometric method (1928), which was then used, is not highly accurate within the range of concentrations studied. It was difficult completely to ensure that the prepared sea water used for making standards was ammonia-free. Though absolute accuracy may have been none too good, the relative precision of measurement between duplicates compared at the same time not only with standards but with one another was much better. Frequently the difference between duplicates or triplicates amounted to 0·7 mg.-atom/m.^{3} or more. Notebook comments such as 'results ignored; high figures attributable to contamination' were frequent. Such an analytical distribution is very reminiscent of that for iron.

Again, Redfield & Keys (1938) made a series of most careful analyses in the Gulf of Maine by the vacuum distillation technique of Krogh (1934). They remark that 'to be reliable, all determinations must be made in duplicate, since unforeseen contamination frequently occurred'. In other words, duplicates did not agree. Further (p. 87), they say: 'The distribution of ammonia appeared very irregular when the observations were first made.... It appeared, however, that great differences might be observed in similar situations at any time and in the same situation at different times.'

One is entitled to question whether these erratic results were really due to analytical error or contamination.

In April and May 1936 in Japanese coastal waters very many analyses were made by the research vessel *Syunpū Maru* (1938). The text is in Japanese, but the table of results has English headings. The distribution of temperature, salinity, density, oxygen, pH, silicate, phosphate, nitrite and nitrate agree with what might be expected of dissolved substances in shallow, partially stratified, temperate waters in spring. On any accepted view of the distribution of dissolved substances, the many results for iron and ammonia are chaotic even at stations which were isothermal and isohaline. The iron results now fall into line with the picture of particulate iron drawn for the English Channel. Is it reasonable to ascribe the Japanese results for ammonia also to a particulate distribution?

In spite of determined efforts by a large number of workers, no nitrifiers able to oxidize ammonia to nitrite have ever been found in sea water as such. These attempts are listed by Carey (1938) and ZoBell (1946, pp. 151–53). Nitrifying organisms have, however, been found associated with bottom deposits and with animal and plant plankton collected near shore in relatively shallow places (Waksman, Reuszer, Carey, Hotchkiss & Renn, 1933; Carey, 1938).

When Harvey (1940) presented diatom cultures with mixtures of ammonium- and nitrate-*N*, analysis showed that, in the light, ammonium-*N* was preferentially removed whereas in the dark the content of ammonium-*N* in the culture as found by analysis remained unchanged. Nevertheless, the dark experiments were compatible with some of the ammonium-*N* having been adsorbed by the cells whilst remaining accessible to bulk analysis of the water including everything in it.

A possible key to the riddle is provided by the work of Lees & Quastel (1946) on soil nitrification of ammonia. They concluded that soil ammonia is held on the surfaces of the soil crumbs by base-exchange combination and that the nitrifying bacteria proliferate only at the expense of such adsorbed ammonium cations. Some such adsorption of part of the ammonia in sea water upon particulate matter would provide an explanation of the experimental findings more reasonable than the exasperatingly frequent 'contamination'. Undissociated ammonia (NH_3) and ammonium-ion (NH_4^+) are present in sea water in not dissimilar amounts (Cooper, 1937) so that adsorption of either might occur.

All these observations may be brought within the following working hypothesis. In the sea ammonia is formed by the breakdown of amino- and amido-*N* in decaying matter, most of which is particulate. It may not be immediately given up to the water but may be retained on the surfaces of the particles as adsorbed ammonia (NH_3), ammonium-ion (NH_4^+) or conceivably as a weak, readily hydrolysable amido-grouping ($—CO.NH_2$). Such particles with densities slightly different from that of the water will accumulate in the surface or bottom strata of the water mass or may be entrained by interfacial tension in the sea surface itself. None the less, their adsorbed ammonia would be determinable by any of the methods of analysis for dissolved ammonia. On such particles—perhaps nowhere else—nitrifying bacteria may find not only a structure on which physically to support themselves as seems necessary in soils but also the ammonium substrate they need. Success in culturing nitrifying bacteria would therefore demand a particulate rather than a plate technique. Ammonia added in solution to phytoplankton cultures would tend of itself to become adsorbed upon the plants in a way which would only be revealed if the plants were removed before analysis. Such capacity of ammonia-*N* for preferential adsorbtion would make it a more favourable plant food than nitrite or nitrate.

If the possibility of removal of ammonia from the aqueous phase of sea water by adsorption upon particles be admitted, 'contamination' as an explanation of the failure of replicate analyses to agree is no longer necessary. Occasionally it must occur, but more often results would be due to random distribution of 'particulate ammonia' of the type now known to apply to iron.

Though this hypothesis gives a coherent explanation of a number of observations, previously somewhat intractable, it is none the less highly speculative. It is put forward here since an opportunity for the writer to test it for himself is unlikely to arise in the near future.

SUMMARY

The hypothesis is proposed that inorganic ammonia may be adsorbed on particulate matter in the sea. The random distribution of such particulate ammonia would account for the frequent 'contamination' reported in ammonia analyses and for the finding of nitrifying bacteria associated only with particulate matter, but never with sea water itself.

ADDENDUM

The Editor has shown me the proofs of a contribution to this Volume (pp. 360–79) by S. M. Marshall & A. P. Orr (1948) on the effect of different plant nutrients upon the phytoplankton in Loch Craiglin. In certain experiments added nutrients disappeared from the water of this shallow loch very rapidly indeed. This suggested to the authors either that the nutrients were speedily absorbed by the phytoplankton and fixed algae, or that they were adsorbed by mud or suspended dead particulate matter. For salts of ammonia, notably the experiments of 2 April 1945 and 10 January 1946, the second view accords with the hypothesis here presented. Dr Orr (*in litt.*) states that Dr Steemann Nielsen in informal discussion has expressed the same idea to Dr Marshall. The uncertainty inherent in analytical data for nitrate allow of no conclusion at present as to possible particulate distribution of adsorbed nitrate in the sea. Such a distribution must be considered unlikely until positive evidence can be produced in its favour. There is nothing in the known distribution of phosphate in the open sea to lend support to a particulate hypothesis for this nutrient on the scale required by the Loch Craiglin results. None the less it would be of interest to know whether the moorland stream or burn brings any considerable amount of iron into Loch Craiglin and, if so, whether ferric phosphate might be formed and precipitated. The pH of Loch Craiglin varied widely during the investigation and, as will be seen from a companion paper to this, ferric phosphate is more likely to be formed when pH is low.

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PHOSPHATE AND FISHERIES

By L. H. N. Cooper, D.Sc., F.R.I.C.
Chemist at the Plymouth Laboratory

(Text-figs. 1–3)

A number of links in the food chain intervene between the presence of nutrient salts over fishing grounds and the marketing of commercial fish. Indeed not a chain but a network provides the better metaphor. The necessary study of each and every mesh must occupy many years. None the less as an empirical short cut it is well worth while to examine quantitatively whether a change in the nutrient resources of an area may be reflected in commercial landings.

The purpose of the paper is not to make positive assertions of fact but to suggest possibly valuable lines of investigation.

PHOSPHATE AND THE SPURDOG

There are four ports exploiting the Eddystone-Lizard grounds of which International Hydrographical Station E1 is more or less the centre. Returns from the port of Plymouth and, to a lesser degree, Brixham are likely to be vitiated from the point of view of this study by landings from deep-sea trawlers operating on occasion hundreds of miles from their home port. The fishery of the port of Mevagissey is, however, carried on by small craft almost entirely on the Eddystone-Lizard grounds. Throughout this paper the serious limitations inherent in all fisheries statistics taken at small ports must constantly be borne in mind. Market conditions at Mevagissey sometimes lead to concentration of all effort on the capture of one species.

It was immediately apparent that dogfish landings at Mevagissey would repay study (Fig. 1, curve *A*). The species there completely dominant in the landings is the spurdog, *Squalus acanthias* (= *Acanthias vulgaris*), which, though classified with other dogfish in the fisheries statistics as demersal, is in fact truly pelagic. It is caught by an autumn line fishery on the Eddystone-Lizard grounds and is often landed by drifters working the winter drift-net fishery from Plymouth.

S. acanthias is noteworthy in that the eggs are developed into young fish within the mother (Ford, 1921) so that the young are never exposed to the vicissitudes of an independent planktonic existence.

The steady increase in landings between 1921 and 1926 might have been due to increased intensity of fishing, change in fishing gear or market conditions. That these cannot account for the whole of the increase is shown by the ratio of landings of dogfish at Mevagissey to (i) the total weight of demersal fish other than dogfish landed at Mevagissey (Fig. 1, curve *B*), and to (ii) the total landings of dogfish (all species) at English and Welsh ports (curve *C*). Both ratios show the same trends as curve *A* suggesting that the increased landings

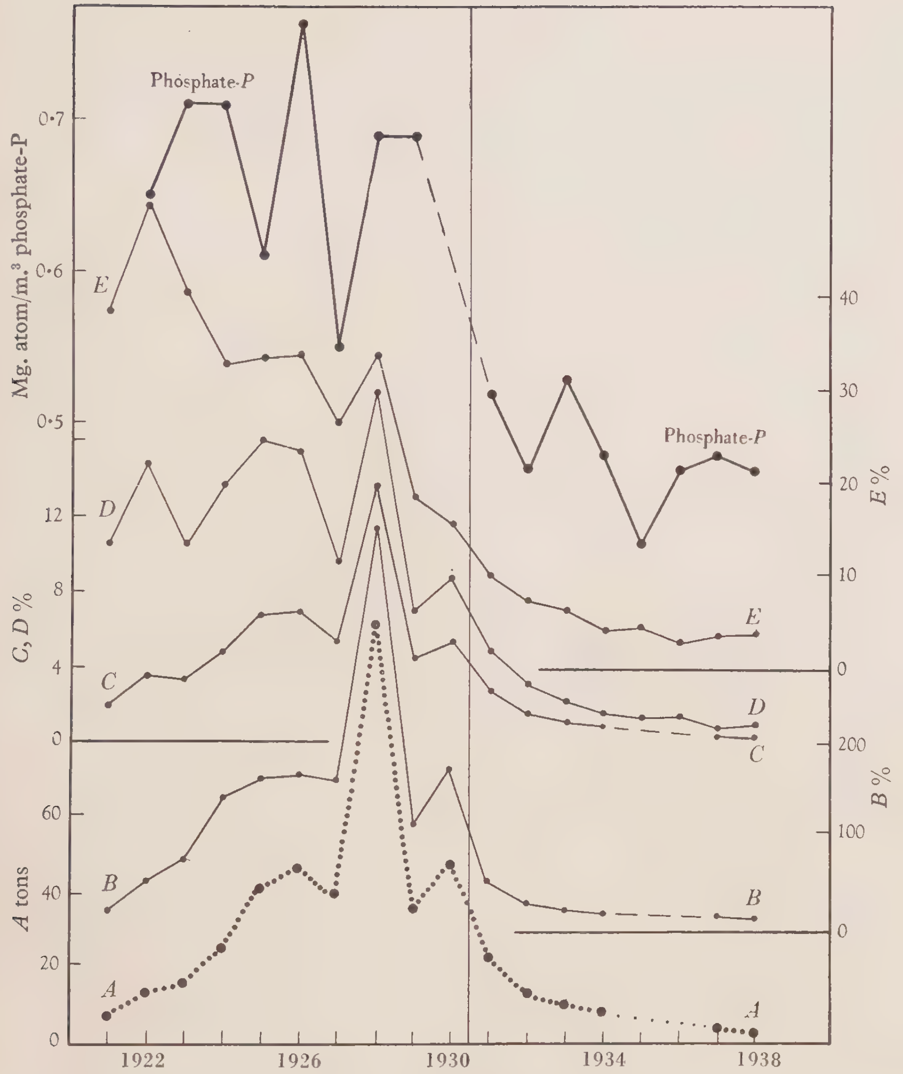

Fig. 1.

A, weight of dogfish landed at Mevagissey (tons).

B, percentage ratio: $\frac{\text{Dogfish landed at Mevagissey}}{\text{Total demersal fish less dogfish landed at Mevagissey}}$.

C, percentage ratio: $\frac{\text{Dogfish landed at Mevagissey}}{\text{Dogfish landed at English and Welsh Ports}}$.

D, percentage ratio: $\frac{\text{Dogfish landed at Brixham, Plymouth, Looe and Mevagissey}}{\text{Dogfish landed at English and Welsh Ports}}$.

E, percentage ratio: $\frac{\text{Dogfish landed from the English Channel (Areas VII D and E)}}{\text{Dogfish landed at English and Welsh Ports}}$.

Phosphate-*P*, mg.-atom/m.³, maximum content at E 1 in preceding winter.

The vertical line marks the change-over from predominantly phosphate-rich (*elegans*) to phosphate poor (*setosa*) conditions.

do reflect an increase in the stock of spurdogs on the Eddystone grounds. In 1928 the dog-fishery was altogether exceptional so that it would seem that the resources of the port were concentrated on this one lucrative fishery at the expense of all the others. Consequently, the 1928 landings probably accentuate the size of what was undoubtedly a very rich stock.

In 1931 and later years the Mevagissey spurdog fishery fell away catastrophically, so that by 1938 landings were a mere one-thirtieth of what they had been in 1928.

The landings for Mevagissey, Looe, Plymouth and Brixham taken together were next examined, though the Plymouth and Brixham returns may include fish caught far from the home port. In Fig. 1 (curve *D*) is shown the ratio of landings to those at all English and Welsh ports. Though the increase in the nineteen-twenties is much less marked than at Mevagissey alone, the relative fall during the nineteen-thirties was felt equally severely by all four ports. It is quite clearly not due to any fall in the national demand for dogfish or to over-fishing.

Again curve *E* shows the ratio of landings of dogfish at all Channel ports, English and French (areas VII D and VII E), to those at all English and Welsh ports. The same behaviour is to be seen though it has to be remembered that other species of dogfish are prominent in the catches at the eastern end of the Channel and may account for the relatively better results in the early nineteen-twenties.

A similar very marked fall about 1930 is shown by the weight of fish landed at Channel ports by steam trawlers (i) per day's absence from port, and (ii) per 100 hr. fishing and by motor liners (Fig. 2).

Also in Fig. 1 (curve Phosphate-P) is shown the winter maximum of phosphate at station E1. Is it coincidence that the falling off in spurdog landings after 1930 accords so closely with the falling off in the stock of phosphate? The relatively poorer nutrient conditions at midwinter 1926–27 are also mirrored in reduced catches in 1927 though this agreement may be fortuitous.

Further understanding of this apparent association of *S. acanthias* with phosphate-rich water may be sought along two lines. Either, (*a*) *S. acanthias*, though an active far-ranging pelagic fish, markedly and directly favours high-phosphate western 'elegans' water of which it would then be an indicator; or, more probably, (*b*) the association traces directly through shoals of clupeoids and mackerel which it attacks and voraciously devours. A correlation exists between herring and phosphate. Presentation of this demands first a study of the 'fine structure' of phosphate distribution which will be attempted in a later paper. Pilchard eggs frequently occur in water of a very poor type (Russell, 1937–40). A quantitative study of the abundance of *S. acanthias* associated with shoals of (*a*) the (eastern) Channel race of herring, (*b*) the 'western' race of herring (Ford, 1928), (*c*) pilchard and (*d*) mackerel might therefore lead to an advance on the central problem of productivity.

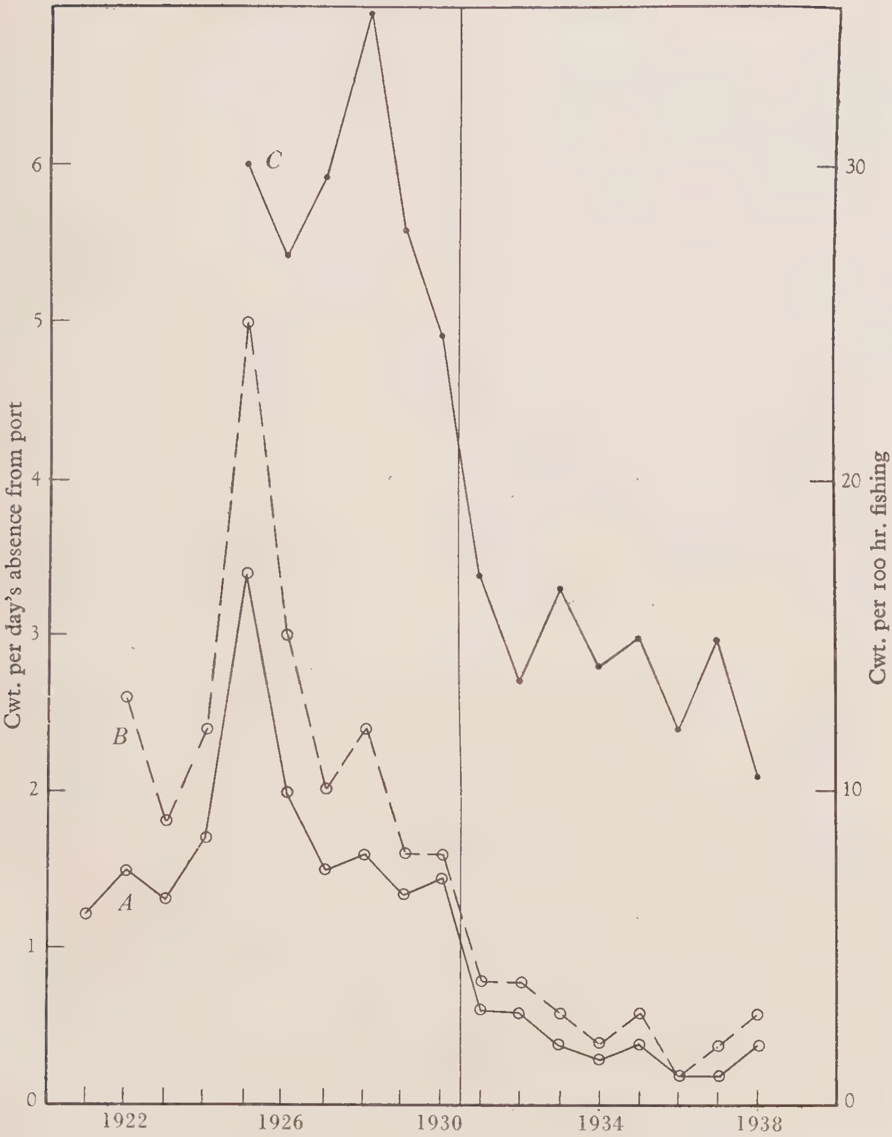

Fig. 2. Landings of dogfish (cwt.), at English ports in the English Channel from:

A, steam trawlers per day's absence from port.
B, steam trawlers per 100 hr. fishing.
C, motor liners per day's absence from port.

The vertical line marks the change-over from phosphate-rich (*elegans*) water to phosphate poor (*sctosa*) water.

Phosphate and Rays and Skates

No immediate connexion would be anticipated between quantity of bottom fish feeding on bottom invertebrate fauna and short-period changes in nutrients in the overlying water. A long-period correlation with a considerable time lag might be expected however.

In an enclosed bio-hydrographical system a steady state should be reached when the amount of phosphorus being added to the bottom deposits as faeces, living or dead organic matter and adsorbed or insoluble phosphate (such as ferric phosphate) would equal the amount of dissolved phosphate returned from the bottom to the overlying water. If now this overlying water mass should be replaced by one richer in nutrients and of greater biological fertility, the rate of deposition of faeces and dead plant and animal remains should increase. In course of time the bottom deposits should become enriched and able to support a larger invertebrate in-fauna and more demersal fish. If, after a period of years, the richer water is itself replaced, this time by nutrient-poor water, the enriched bottom deposits would continue able to support the increased population for some years to come. Finally, the reserve store would become exhausted and the stock of bottom-dwelling animals would decline. These changes should be reflected in the fishery statistics.

Teleosts have pelagic young immediately and directly influenced by a change in the fertility type of the overlying water. Moreover, they may voyage far before being caught on our grounds. The abundance of mature teleosts therefore may depend upon opposing conditions for survival in their larval and adult stages. No clear picture would be expected. By contrast, rays and skates have no pelagic young so that at no stage of their existence is their survival dependent directly upon the character of the overlying water. Their survival must be dependent solely upon the fertility of the bottom deposits. Again, the juvenile thornback ray, *Raia clavata*, does not migrate and the mature adults are little more enterprising (Steven, 1936). If this is true generally of all rays, as it probably is, then they ought to reflect closely the balance between the productivity of the sea bottom in the neighbourhood of Plymouth on the one hand, and intensity and efficiency of fishing on the other.

We suspect on rather slender evidence that our waters were poor in phosphate in the early part of this century and that the enrichment occured about 1921 and we know with certainty that poorer conditions returned to the overlying water at the end of 1930 (Matthews, cf. Cooper, 1938) (cf. Fig. 1, curve *P*). If the argument is sound, some years would have had to pass before the enrichment of the water was reflected in increased catches of rays. Similarly, once the stock of fish and bottom food was built up, a lucrative fishery should have persisted for some time after the rich water had departed.

With this hypothesis in mind the landings of rays and skates at Mevagissey between 1921 and 1938 were examined (Fig. 3, curve *F*). The drop in landings

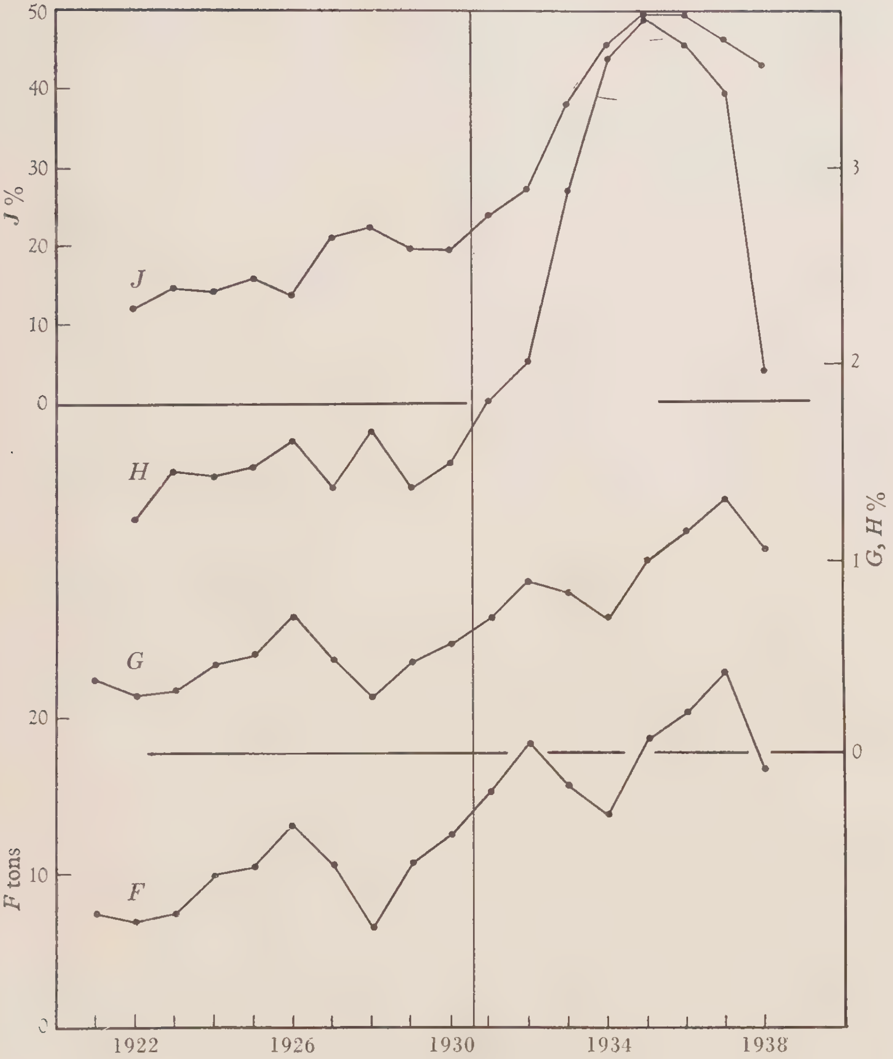

Fig. 3.

F, landings of rays and skates at Mevagissey (tons).

G, percentage ratio: $\dfrac{\text{Rays and skates landed at Mevagissey}}{\text{Rays and skates landed at all English and Welsh ports}}$.

H, percentage ratio: $\dfrac{\text{Rays and skates landed at Plymouth}}{\text{Rays and skates landed at all English and Welsh ports}}$.

J, percentage ratio: $\dfrac{\text{Rays and skates landed at Plymouth}}{\text{Demersal fish other than rays and skates landed at Plymouth}}$.

in 1928 may very probably be accounted for by the evident concentration of the port on the exceptional stock of spurdogs in that year and not to any decline in the ray population. We see that landings increased reasonably steadily from 1921 to 1937. That this reflected a real increase in the stock of fish is suggested by curve *G* which depicts the ratio of landings of rays and skates at Mevagissey to those at all English and Welsh ports.

The port of Plymouth had a similar experience though the main increase in landings there appeared between 1932 and 1934 (curve *H*). This sharp rise suggested a possible improvement in fishing methods, perhaps the introduction of the Vigneron-Dahl trawl on the large steam trawlers. That this was not so is indicated by curve *J* showing the ratio between landings of rays and skates to total demersal fish other than rays and skates at Plymouth. The same rise in the early nineteen-thirties is apparent; if it were due to use of an improved trawl, increased landings of all demersal fish would have been anticipated and the ratio should have remained unchanged.

Though this confirmation of our hypothesis is striking, so many factors enter into the success of a fishery that it cannot be considered as proved without much further evidence.

For this study, landings at the port of Newlyn 40 miles to the west of Mevagissey were intentionally ignored, since there are no nutrient salt data for the area. We do know that 'elegans'-type water must more often overlie the grounds fished from Newlyn than those fished from Mevagissey. On the above hypothesis alternation of rich and poor conditions would therefore be expected to be much less marked on the more western grounds.

There has in fact been a decline in the landings of rays and skates at Newlyn (Steven, 1932, p. 26) and the conditions of the fishery have become much more onerous for the men. This may be due to over-fishing or it is just possible that the fish, of non-migratory habit though they be, had moved up-Channel towards the grounds which we have *postulated* to be newly enriched.

Phosphate and the Invertebrate Bottom In-fauna

If the above hypothesis is correct, an important rider follows. Practically all bottom-dwelling invertebrates have planktonic larvae. We know from Russell's work (1937–40) that the conditions for survival of zooplankton deteriorated sharply in 1931 and in subsequent years became steadily worse. This seems to be true for all species without exception. The number of larvae of bottom invertebrates surviving to settle and metamorphose on the bottom must therefore have been considerably less in the nineteen-thirties than in the nineteen-twenties. Once successfully metamorphosed and established in their adult home they should have found richer food for which there would have been reduced competition. Each single organism had therefore the opportunity to grow to a larger size. In the first place this argument applies to detritus feeders. Probably it may be extended to the whole of the bottom in-fauna, but not necessarily to the members of the epi-fauna taking their food by filter-feeding mechanisms and the like from the overlying water. The rider is therefore that during the nineteen-thirties the in-fauna probably decreased in numbers but that each organism became relatively larger.

No estimate can be made as to whether the *mass* of invertebrate food available for demersal fish changed for better or worse. An increase in the average size of the prey might however adversely affect the ability of small fish to catch and swallow their food, leading to relatively greater mortality during the first years of life.

The improvement in the ray fishery discussed above would suggest that the mass of food must have increased. As against this the adverse conditions for the pelagic young of teleost fish and of carnivorous invertebrates may have resulted in the rays being subjected to less severe competition for the available food.

That arguments such as these, by themselves, prove nothing needs to be stressed. As Mr G. A. Steven has remarked to the writer, we have no positive evidence that food supply is dominant amongst the many factors which may govern the survival and numbers of elasmobranch fish. A single coincidence between the stock of a nutrient in the water and the landings of a commercial fish may be due to chance or to some associated more fundamental but unrealized variable. Phosphate itself, primary though it is as a *plant* nutrient, is better regarded as an indicator of water type comparable with salinity. Though water with a high content of phosphate and probably of other nutrients and growth-promoting substances has the potentiality for producing a greater biomass than one with a lower content, it need not be better fitted for a particular species of animal and the food on which it feeds.

Fertilizing the Ocean

There is nothing new in the idea that the productivity of a limited body of water may be improved by adding plant nutrients, and in some circumstances it may be economic as in carp ponds and Norwegian oyster pools. That enclosed arms of the sea may be treated in the same way is now the subject of study by Gross and his colleagues (1942–6) and shows distinct promise. To fertilize considerable areas of the open sea provides a fascinating theme for dialectic with little factual data for a real assessment. Ritchie (1944), with a natural distaste for the compulsory restriction or moderation of fishing activity which is the remedy for over-fishing offered by fisheries naturalists, proposes that the International Council should arrange the allocation of sums of money contributed by the several nations for chemical nutrients with the assurance that these distributed in the sea will support a larger fish population and an increased rate of fishing. Qualitatively none would disagree with this proposal which has received approval, unsupported by figures, from experience of the fisheries of Mauritius (Wheeler, 1945). Quantitatively the idea seems hopelessly uneconomic and has been assailed by Graham (1944) and by

Atkins (1944) on account of the 'mountainous' amounts of phosphate and other nutrients which would be needed. Ritchie riposted with figures which do not bear examination. He pointed out that 201,000 tons of phosphatic nutrients (as P_2O_5 which equals 88,000 tons as P) were used in agriculture in the United Kingdom and Eire in 1937 and that this is considerably in excess of the phosphate turnover in the English Channel. Maybe, but the phosphate *added* to the land helped to produce about 42,000,000 tons of crops and supported 12,900,000 cattle as well as numerous horses, sheep and pigs (figures are for 1939 from Whitaker's *Almanac*, 1941, pp. 632 and 704). The same amount of phosphate *present* in the English Channel in 1937 resulted in the landing of 76,000 tons of fish. Though doubling the amount of phosphate and other nutrients in the Channel might more than double the amount of fish, there remains an enormous gap to be closed between 76,000 tons of fish and 42,000,000 tons of crops plus millions of stock animals.

The very low economic efficiency of utilization of phosphate in the sea may be illustrated by the following figures.

McCance & Shipp (1933, table A) published large numbers of analyses of phosphorus in cooked fish flesh which were surprisingly uniform, around 0·25 % of the weight of cooked edible flesh. Allowing a 20 % loss in weight on cooking, this becomes about 0·2 % of the raw flesh, a figure confirmed by a few analyses of raw fish fillets in their table H. The offal from the fish, mainly head, bones and gut will contain more phosphorus than the flesh, as was shown by the analyses of whitebait and sprats which were cooked whole. Though the fish curing or processing factory will be likely to convert its offal into agricultural fertilizers, domestic offal and that from retail shops will go to the rubbish bin. Only phosphate in fish flesh is of value to the domestic consumer. The significant ratio is thus:

$$\frac{\text{Phosphorus in fish flesh}}{\text{Wet weight of whole fish}}.$$

If two-thirds of the wet weight of the fish is considered to be edible flesh, this ratio will be $2/3 \times 0{\cdot}2\,\%$ wet weight of whole fish $= 0{\cdot}13\,\%$. This figure, though not very accurate, is a sufficient measure of the usable phosphorus recovered from the sea in fish and may be combined with figures for total landings of marketable fish to give a measure of the efficiency of recovery of phosphorus from the sea. Data for the years 1925–37 have been extracted from the *Bulletin Statistique* for areas VII D + VII E (English and French Channel ports). The area of the English Channel is about 82,100 sq.km. and its average depth about 72 m. Its volume is therefore about $5{\cdot}9 \times 10^{12}$ cu.m. To derive a round figure for the phosphate available for plant growth, the winter maximum for station E 1 has been assumed to represent an average figure for the whole of the Channel, enabling the total phosphate content of the Channel to be calculated for each year. The ratio of edible phosphorus in marketable fish to the available stock of phosphorus in the water has then been calculated.

Year	Weight of fish landed (tons)	Edible phosphorus in fish landed (tons)	Phosphorus available for growth in Channel (tons)	Usable phosphorus landed as percentage of phosphorus available for growth (%)
1925	81,000	115	111,000	0·104
1926	79,000	103	137,000	0·075
1927	74,000	96	100,000	0·096
1928	71,000	92	126,000	0·073
1929	95,000	123	126,000	0·098
1930	58,000	75	—	—
1931	76,000	99	95,000	0·104
1932	88,000	114	86,000	0·133
1933	95,000	123	97,000	0·127
1934	93,000	121	88,000	0·137
1935	65,000	85	77,000	0·110
1936	79,000	103	86,000	0·120
1937	76,000	99	88,000	0·112

Thus, during many years of intensive fishing, each year 0·1 % of the available stock of phosphorus has been recovered in a form usable by man. Though the fertility of the water might well be increased rather more than in proportion to the amount of fertilizer added, the prospect of dumping phosphate in a body of water such as the Channel appears most unattractive. Even if the efficiency of recovery could be increased ten times, the yield would still be much less than could be got from the soil dressed with the same amount of fertilizer.

As matters now stand, very large amounts of nutrients are being poured into the sea, the great sink, as sewage from coastal towns and by way of the rivers from inland towns and farms fertilized and unfertilized. Phosphorus is a very precious commodity which in not so many years will become very scarce. The scale on which phosphorus even now is being dissipated to the sea is more than the world can afford. In years to come the cry will be for more methods for recovering phosphorus from the sea, not for putting it in.

Millennia ago, nomadic man, realizing that hunting was an uncertain and wasteful method of gaining a livelihood, changed to an economically far more efficient, pastoral and agricultural existence. Fishing remains as the major hunting pursuit still followed by civilized man. If it is to become more productive it must cease to be feral and become pastoral. To that extent I agree with Ritchie. But an efficient exploitation of the soil—or the sea—demands full control of weeds and pests which otherwise take an undue share of any plant nutrients added. Until fishing becomes pisciculture, and weeding of unwanted algae and control of unwanted pests, i.e. competitive predators and parasites, take their due place, fishing can never be more than ruthless and non-selective hunting.

The writer wishes to express his indebtedness to Mr E. Ford and Mr G. A. Stevens for stimulating discussions and pertinent criticism.

Summary

Landings of the spurdog, *Squalus acanthias*, at Mevagissey reflect the changes in phosphate at the neighbouring International Hydrographic Station E1.

It is suggested that commercial landings of rays and skates ought to follow major changes in nutrient content of the overlying water with a time lag of some years. Fishery statistics for English Channel ports support this view. The dependence of the bottom in-fauna upon the fertility of the overlying water is also discussed.

Proposals to improve commercial fisheries by artificially fertilizing considerable areas of the open sea are critically examined. Such artificial enrichment is considered to be grossly uneconomic unless fishing becomes pisciculture in which weeding of unwanted algae and control of unwanted pests—competing predators and parasites—is undertaken.

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THE ESTIMATION OF PHOSPHATE AND OF TOTAL PHOSPHORUS IN SEA WATERS

By H. W. Harvey, Sc.D., F.R.S.
Hydrologist at the Plymouth Laboratory

(Text-figs. 1–11)

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The Estimation of Phosphate

Description of an Absorption Meter

During an investigation of the total phosphorus (present as dissolved phosphate, dissolved organic phosphorus compounds, microplankton and suspended detritus) in samples of sea water, it became necessary to estimate phosphate in solution by an objective method. Estimation by eye of the molybdenum blue formed in the Atkins-Denigès method of analysis appeared to vary in precision from day to day; moreover, it was quite unsatisfactory in waters made turbid with added bacteria or other organisms.

Discussion with Dr W. R. G. Atkins, F.R.S., indicated that any method was to be avoided which measured the change in intensity of illumination falling on a photoelectric cell because very small voltage changes would have a considerable effect on the intensity of the light source. Such an instrument would not only need calibration, but this might change with time as the characteristics of the cell altered. The desiderata were defined as:

(1) The use of balanced photoelectric cells, the light falling upon them being kept constant except for fluctuations in intensity of the light source, which are not easily avoided.

(2) Fluctuations in the intensity of the light source to have no effect upon the null point.

(3) Any change with time in the characteristics of the photocells to become at once obvious and correctable.

(4) Readings in units directly proportional to the light absorbed by the molybdenum blue formed on adding stannous chloride to the liquid, and not based on a calibration curve.

It was also desired that no more than 70 c.c. of liquid should be sufficient for a measurement to be made.

A simple instrument has been developed which meets these requirements (Fig. 1). The observation tube T is filled with water and reagents; the slide, carrying lamp and photocell P_2, is then moved until no current flows through the galvanometer. The distance of lamp from P_1 is measured and the pointer on the slide set to read the *virtual* distance of L to P_2 on a logarithmic scale.

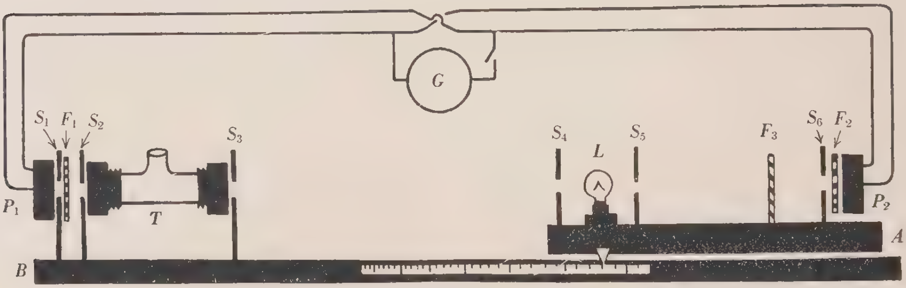

Fig. 1. Photoelectric meter. A, slide on which lamp and P_2 are mounted. B, base, 120 cm. overall length, on which P_1 and T are mounted, carrying scale showing logarithm of virtual distance of lamp from P_1. F_3, neutral filter made from two glass plates with smoked faces. G, galvanometer 483 ohms resistance, 2 sec. period, 200 mm. per μA. deflexion. L, lamp, car headlight 48 W. 12 V. with coiled filament in shape V, *circa* 4 mm. from corner to corner, held in bracket which is earthed, and operated through a dimming switch. P_1, P_2, selenium photocells, 23 mm. aperture, made by Evans Electroselenium Ltd., Bishop's Stortford. F_1, F_2, red light filters, Ilford 608 Spectrum. S_1 to S_6, light stops, diameter of aperture $\frac{1}{2}$ in. in S_1, $\frac{17}{32}$ in. in S_2, $\frac{7}{16}$ in. in S_3, $\frac{1}{2}$ in. in S_6. T, observation tube, glass $\frac{7}{8}$ in. internal diameter 15 cm. long with ground ends against which windows are held, having a thin coat of vaseline between the ground glass and window surfaces; the windows are removable for cleaning.

Since the 15 cm. observation tube is filled with liquid with refractive index *c.* 1·4, the virtual distance is some 4·3 cm. less than the actual distance. Thus if the actual distance were 80·0 cm. when no deflexion was shown on the galvanometer the virtual distance would be 75·7 cm. and the reading (or log d_0) 1·8791.

Stannous chloride is then added, the liquid replaced in the tube, and when the blue has fully developed the slide is moved towards P_1, until no current flows through the galvanometer. The virtual distance of lamp from P_1, or log d_1, is then shown by the pointer.

The increase in absorption of light passing through the 15 cm. column, due to the formation of molybdenum blue, is

$$\frac{d_0^2}{d_1^2} = 2\,(\log d_0 - \log d_1) \quad \text{or} \quad 2\Delta,$$

and the extinction coefficient of the molybdenum blue formed in the solution

$$E_{\text{cm.}} = \log_{10} \frac{\text{incident light}}{\text{transmitted light}} \text{ per cm. length of column}$$

$$= \frac{2 (\log d_0 - \log d_1)}{15} \quad \text{or} \quad \frac{\Delta}{7\cdot5}.$$

The value of Δ is a direct measure, strictly proportional to the increase in blue colour in the solution, brought about by adding the reductant.

The value of the extinction coefficient needs further qualification. It changes with the wave-length of light, and therefore with both the composition of the red light transmitted by different filters and with the sensitivity of the photocell within this wave band. It is different if the same red filter is used with a different kind of photocell, or the eye, and it is different if the same photocell is used with another red filter which transmits light of different spectral composition.

Readings of $\log d_0$ and $\log d_1$ can be made to within 0·0005 on the scale; thus the instrumental error in values of Δ does not exceed ±0·001. The colour formed in sea water due to the presence of 1 mg. phosphate-P per m.^{3} requires a movement of *c.* 0·0040 on the scale ($\Delta = 0\cdot0040$). Hence the instrumental error does not exceed that attributable to ±0·25 mg. P per m.^{3}

Adjustment of the absorption meter is carried out as follows. The lamp filaments and stops S_3, S_2 and S_1 are carefully aligned with the slide in its nearest and farthest extreme positions, by observing the shadows cast by the stops with the light filters and photocells removed. The observation tube is inserted and the annularity of the light ring cast on S_1 checked by inspection.

The photocells and light filters are replaced and the slide moved until no current flows through the galvanometer. After the light has been on for several minutes the slide is readjusted to zero current (or null point) position and the light dimmed by the dimming switch. The galvanometer will show a deflexion as the light dims, coming back to zero as the light fades out. This appears to be caused by the two photocells differing in either their 'change in sensitivity with illumination', or in the speed with which they attain constant potential. When due to the former it can be remedied.

The sensitivity of a selenium cell changes if the illuminated area on its surface is moved. The 'change in sensitivity with illumination' likewise changes, but to a lesser extent.

To remedy the change in null point with change in intensity of light source, it was sufficient to move the stop S_6 in the vertical plane. This allowed the two photocells to be matched with respect to this characteristic. This having been done, slowly dimming the light source had no effect on the null-point position. Once matched the photocells appear to remain matched. In another similar instrument, an alternative method was used. A resistance was interposed between the galvanometer and one of the photocells; this also necessitated altering the neutral filter F_3.

Two further properties of selenium photocells require consideration. If one cell is illuminated much more brightly than the other for more than a few seconds, it will fatigue and require a short time to return to equilibrium. There is no need to let this happen, because after the tube has been refilled with another sample, the lamp is turned on slowly through the dimming switch while the slide is being moved towards the new null-point position.

After the photocells have been in the dark for some time (as when the apparatus has not been in use), they require a short period to attain a full response after the light is switched on. In consequence the null point changes during the first 1 or 2 min. However, if the cells are illuminated (equally) for 10 min. and the light is then switched off for a short period, the response is more rapid when the light is switched on again. The null point steadied in 30–40 sec. and remained steady for several hours in a dust-free room.

Owing to this property of the cells the following procedure was adopted. After use, the observation cell is filled with water, replaced, and the slide set at null point, the lamp being then switched off. When next required the lamp is switched on about 10 min. before starting a series of measurements and only switched off for the short periods required for changing the contents of the observation tube.

After the initial alignment and matching of the photocells, the strict linearity of the readings was checked. This is necessary to make sure that (*a*) alignment is perfect at all positions of the lamp and (*b*) there is either no reflexion from the walls of the tube, or that the very small amount of reflected light follows the inverse square law.

The tube was filled with water and reagents and log d_0 noted. Several neutral glass filters were inserted between F_1 and S_2, one at a time, and the d_1 values noted. Then two or more were inserted, and Δ for the combination was found to equal the sum of the Δ's observed for each separately.

A further check was made to be sure the simple theory involved in calculating the virtual distance was obeyed.

The tube was withdrawn and the slide moved until no current flowed through the galvanometer. The *actual* distance between lamp and photocell (d_a) was measured in cm. A neutral filter having an optical density of about 0·4 was then inserted between F_1 and S_2, the slide moved to zero current position, and the actual distance between lamp and photocell (d_b) measured.

The optical density of this neutral filter for the particular wave band of red light and photocell used equals

$$2\,(\log d_a - \log d_b).$$

The filled tube was then replaced, the slide moved until no current flowed, and log d_c, being the log of the *virtual* distance of lamp from photocell, read. The neutral filter was again inserted, the slide moved to the new zero deflexion position, and log d_e noted

$$2\,(\log d_a - \log d_b) \text{ equalled } 2\,(\log d_c - \log d_e).$$

This evidence indicated that the instrument obeyed the simple theory involved. It also satisfied the other initial desiderata.

On the Formation of Molybdenum Blue

When stannous chloride is added to sea water containing ammonium molybdate and sulphuric acid, either no colour is formed, colour is formed only when phosphate is present, or colour is formed when no phosphate is present.

The conditions under which these eventualities take place are shown in Fig. 2.

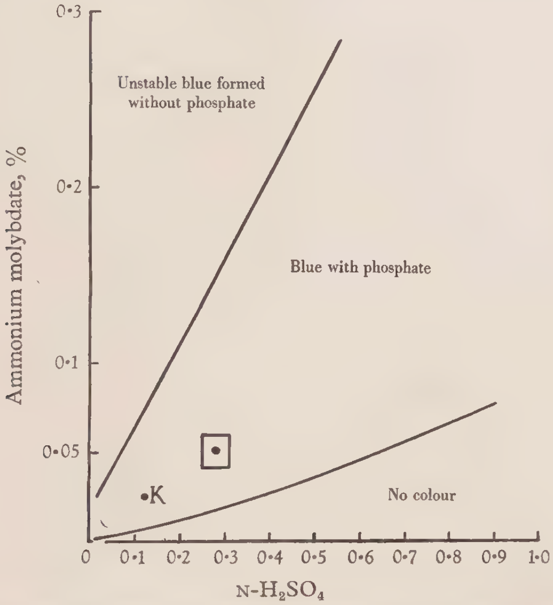

Fig. 2. Diagram showing the effect of varying concentrations of sulphuric acid and molybdate on the formation of blue in sea water, from data by Gripenberg (1929) and Kalle (1934). The point within the square represents the conditions investigated in this communication, the point marked *K* the conditions investigated by Kalle.

The following observations relate to the formation of molybdenum blue in sea water and in very dilute solutions of phosphate to which had been added:

(1) Sulphuric acid, making the solution *c.* 0·28 N with a pH of 0·82.

(2) 0·05 % ammonium molybdate,

and had been reduced by the addition of at least 0·00045 % $Sn^{\cdot\cdot}$.

This corresponds to the addition of 2 c.c. of Atkins-Denigès reagent to 100 c.c. of sea water.

On the addition of stannous chloride, the colour develops rapidly (Fig. 3) and is followed by a relatively slow fading, which becomes still slower as fading progresses.

With phosphate in distilled water colour development is less rapid, and the depth of colour, due to the presence of the same amount of phosphate, is greater than in sea water or salt solution.

In distilled water and in sea water, both the rate of colour development and the final depth of colour produced are greater with increasing temperature, and are greater if more stannous chloride is used, up to but not beyond a limiting quantity.

The blue substance produced in distilled water has a different light-absorption band to that produced in sea water (Buch, 1929; see also Cooper, 1938, who finds that the 'salt error', or ratio of colour produced in distilled water to that produced in sea water, varies with the light filter used).

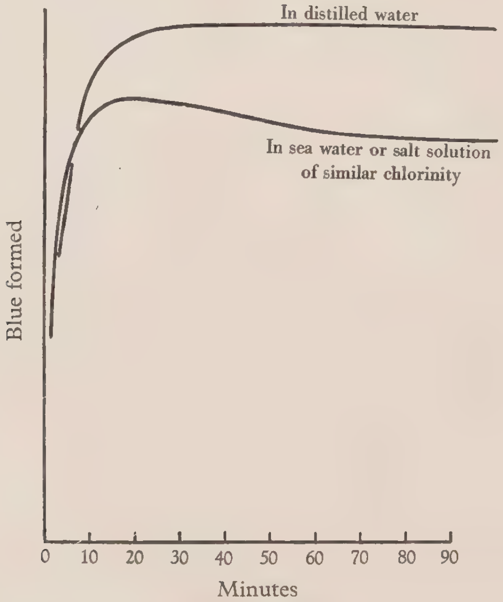

Fig. 3. Diagram showing rate of formation and subsequent fading of blue, due to the same concentration of phosphate in distilled and in sea water, at 10° C.

These blue substances have colloidal properties. The molybdenum blue formed by mixing trivalent molybdenum with molybdate has been seen to consist of aggregates or micelles of very different sizes (Schirmer, Andrieth, Gross, McClellan & Seppi, 1942) when viewed under an electron microscope. It seems reasonable to assume that the subsequent fading of the blues produced in acid water or acid salt solutions is due to aggregation of colloidal particles or micelles.

A study of these variables which affect the production of the blue substance in sea water containing phosphate was made in order to decide upon a reasoned procedure in carrying out analyses.

Variation in acidity. The effect of relatively small variations in acidity and in molybdate concentration upon the quantity of blue formed in sea water containing phosphate are shown in Fig. 4. It is seen that a 1% increase in acid decreases the colour by about 0·5%.

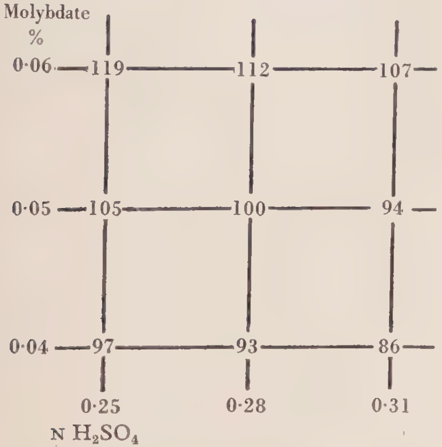

Fig. 4.

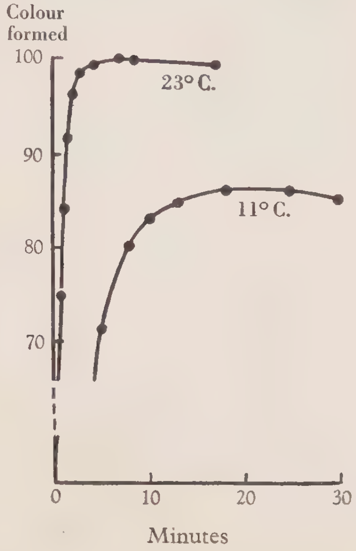

Fig. 5.

Fig. 4. Effect of varying concentrations of sulphuric acid and of molybdate on the blue formed in sea water containing phosphate. The colour produced with 0·05% ammonium molybdate and 0·28 N-acid is shown as '100'.

Fig. 5. Diagram showing the rate of colour formation and the amount of blue developed in the same sea water at 11 and 23° C., after addition of the same quantity of stannous chloride.

Time taken for ionic equilibrium to be attained after adding the acid molybdate to sea water. The following experimental data show that a period of some 3 min. is taken for equilibrium to be attained:

Stannous chloride added	Intensity of blue formed
At once	> 161
After 1 min.	124
3	100
6	99·4
26	100·5
60	100
3 hr.	100
24	95·6

The effect of temperature. Increasing the temperature increases the velocity of the reactions involved. The maximum colour is developed sooner and the interval of time during which the colour is within ±0·5% of its maximum value becomes shorter. (This interval is also shorter if the quantity of stannous chloride is reduced.) Increasing the temperature also increases the amount of blue colour developed (Fig. 5).

With phosphate in distilled water the increase in colour was found to be 0·96% per rise of 1° C. within the range of 8–20° C. This is the same value as found by Kalle (1933) between 5 and 30° C. under the condition indicated in Fig. 2.

With phosphate in sea water the increase was 1·2% per rise of 1° C. in Kalle's determinations, rather less in my own experiments.

The effect of varying the quantity of stannous chloride added. When increasing quantities of $SnCl_2$ are added, the colour developed increases rapidly until about 12 times more Sn than the phosphate-P present has been reached (Gripenberg, 1929). Thereafter there is a slow increase in colour developed. With considerable additions the development of blue in phosphate solution becomes disproportionately greater than in sea water.

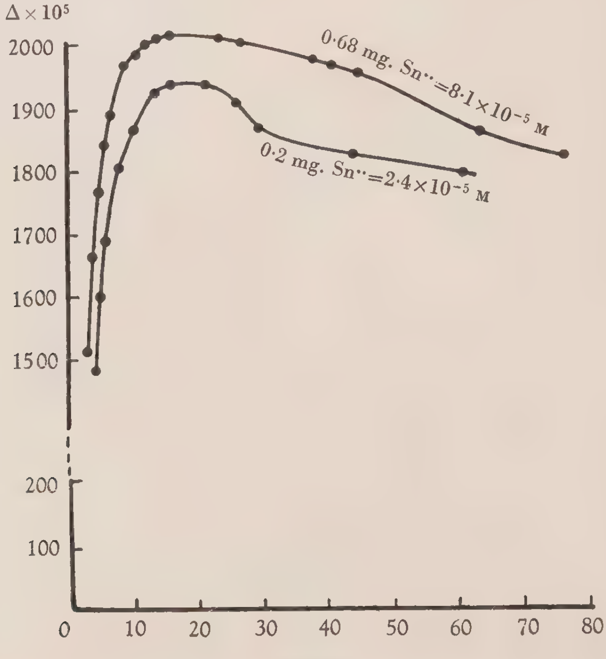

Fig. 6. The formation and fading of blue developed in a sea water, enriched with 40 mg. phosphate-P per m.^{3} at 10·5° C. Upper curve shows the course with 0·68 mg. $Sn^{\cdot\cdot}$ added to 70 c.c. of liquid, lower curve with 0·2 mg.

The present investigation has been confined to additions varying between 0·2 and 0·8 mg. $Sn^{\cdot\cdot}$ to 70 c.c. of liquid—initial concentrations lying between $2{\cdot}4$ and $9{\cdot}6 \times 10^{-5}$ molar $Sn^{\cdot\cdot}$ and not exceeding $0{\cdot}15 \times 10^{-5}$ molar phosphate.

Within this range the increase in colour due to each additional 0·1 mg. $Sn^{\cdot\cdot}$ added amounts to approximately 1%.

Increasing the stannous chloride also increases the velocity of colour formation, and, in addition, delays the onset of fading (Fig. 6).

On mixing with sea water to which acid and molybdate have been added, the stannous ions are rather soon oxidized. By adding N/100 iodine after intervals and back-titrating with thiosulphate, it was possible to follow the fall in concentration of stannous ions (Fig. 7).

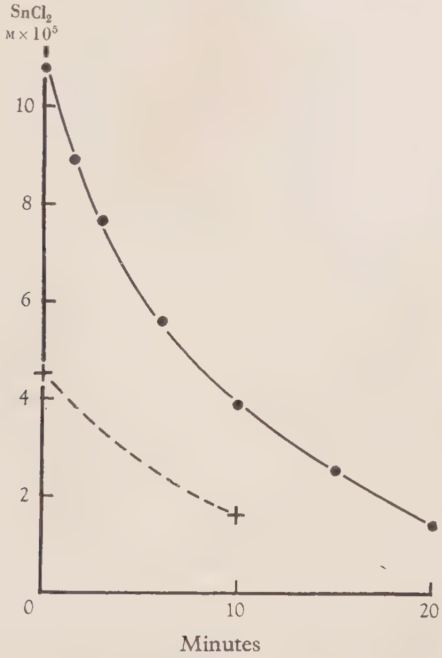

Fig. 7. Diagram showing the rate of oxidation of stannous chloride added to sea water containing 2 % of Atkins-Denigès reagent.

The effect of particulate matter in suspension and of the products of organic decay. The presence of either bacteria or of kaolin in sufficient quantity to make the water just visibly cloudy does not interfere with reasonably exact measurement of the blue formed on adding stannous chloride.

Series of estimations have been made with a sea water in which bacteria had grown after the addition of asparagin in sufficient quantity to raise its absorption coefficient in red light by $E_{\text{cm.}}$ 0·0036. The effect of this particulate matter was to reduce the blue colour formed on adding stannous chloride by 4 %.

A further series of estimations have been made with a natural sea water just visibly cloudy with kaolin, which had entered the sea after heavy rains. There was sufficient in suspension to increase the absorption coefficient of red light of the water by $E_{\text{cm.}}$ 0·009. This had the effect of reducing the blue colour formed by 5 %.

In another experiment a natural sea water was incubated for several days with a considerable quantity of added plankton organisms until they had decayed. After passing through filter paper the water showed no marked cloudiness. Determinations of the increment in blue colour developed due to the addition of 20 mg. phosphate-P per m.^{3} were made in order to find out whether organic decay products affected the production of blue colour. The increment found ($\Delta = 0{\cdot}0832$) at 15° was the same as that in unpolluted sea water ($\Delta = 0{\cdot}0830$) at the same temperature and using the same quantity of stannous chloride.

The effect of varying salinity. It is known that the blue colour formed, due to the same quantity of phosphate, increases in sea waters when the salinity falls below about 25 °/₀₀.

An experiment was made in order to determine whether there was any variation at salinities such as are ordinarily found in inshore and open sea waters:

Salinity (°/₀₀)	Colour formed (mean of determinations in triplicate)
35	100
30	99·5
25	101·8

The rate of fading of the blue colour. Shortly after the colour has reached its maximum, fading is observed. In both sodium chloride solution and in sea water the colour decreases in the next half hour to about 94 % of its maximum value. Thereafter fading is slower (at about half the former rate). When the red light absorbed is plotted against time, a marked inflexion in the curve is apparent, and the shape of the curve during this 30–40 min. differs somewhat from one sea water to another. As already stated, the addition of more stannous chloride delays the onset of fading, but it does not change the general form of the curve.

These observations led to the following hypothesis. Immediately after formation, the molecules aggregate to form micelles and these continue to aggregate—growing larger and fewer. The rate of aggregation, quick at first, slows later. As the molecules aggregate and gradually grow larger, the blue colour fades. The light absorbed by the solution not only becomes less but moves from the red towards shorter wave-lengths. On inspection the fading blue solutions are seen to become both less intense and to acquire a blue-green hue. Addition of 0·05 % of gum arabic, acting as a protective colloid, smooths out the inflexion in the curve as the blue fades while greater additions delay the inception of fading.

That aggregation would cause fading seems certain on considering the situation in reverse, for if particles of a slowly dissolving dye are suspended in water the colour increases as the particles dissolve.

This hypothesis provides an explanation of observed characteristics in the rate at which the blue colour develops.

On the rate at which blue develops. As a first approximation, the light absorption (Δ_t) was taken as proportional to the quantity of phosphate which had reacted at time t during the reaction, since the maximum colour developed (Δ), when the rate of development and fading balance each other, has been found proportional to the phosphate present at the commencement.

Then $\Delta - \Delta_t$ is a measure of the unreacted phosphate concentration at time t; if the logarithm of this is plotted against time an almost linear relation is found. It is almost but not quite linear with phosphate in distilled water, salt solution or sea water.

This indicates that of the several ions taking part in the reaction all but one—phosphate—are in excess. The apparent velocity approaches that of a monomolecular reaction controlled by the concentration of unchanged phosphate ($\Delta - \Delta_t$) present at any moment.

The velocity will tend to depart somewhat from the course of a monomolecular reaction because (*a*) the concentration of stannous chloride is falling throughout the reaction (Fig. 7) and also because (*b*) fading of the blue, due to aggregation of molecules and then further aggregation of the micelles so formed, is not likely to follow the course of a monomolecular opposed reaction.

With regard to (*a*), it is seen from Fig. 6 that increasing the initial concentration of reductant increases the reaction velocity. It would be expected that if the oxidation of stannous chloride by atmospheric oxygen throughout the period of blue formation could be retarded, this would have the same effect. Experiment confirmed this. The addition of sulphite (0·01 M) increased the rate of blue formation. Hence the quantity of stannous chloride present is not in sufficiently gross excess throughout to allow the monomolecular reaction to proceed entirely unaffected.

With regard to (*b*), if fading is most rapid immediately after the formation of blue and does not continue at a rate proportional to the intensity of blue colour during the early part of the reaction (which it does not do, *vide supra*), Δ_t is more than proportional to the phosphate which has taken part in the reaction at time t. In consequence the apparent velocity calculated from this first approximation (Δ_t= phosphate which has reacted at time t) should (i) be greater than the mean velocity early in the reaction while the major part of the blue is being formed, (ii) dwindle for a short period after the initial rapid development of most of the blue while this is most rapidly aggregating, and (iii) indicate a slight rise in apparent velocity towards the end of the reaction after the greater part of the blue has been formed and has had time to undergo its early aggregation. Experiment shows that this is so.

The velocity constant for a monomolecular reaction was calculated for successive intervals of time during the formation of blue:

$$k\,(\text{apparent}) = \frac{2{\cdot}3}{t_2 - t_1} \log_{10}\left(\frac{\Delta - \Delta t_1}{\Delta - \Delta t_2}\right).$$

The following is illustrative.

Time (min.)	Δ_t or light absorbed	Interval (min.)	*k* (apparent)
0	0	—	—
0·935	0·0900	0·933	0·769
1·45	0·1130	0·517	0·604
1·935	0·1285	0·483	0·586
2·47	0·1410	0·533	0·575
3·25	0·1530	0·783	0·540
3·915	0·1595	0·667	0·504
6·0	0·1710	2·083	0·587
8·0	0·1742	2·0	[0·55]
10·0	0·1752	—	—
13	$0{\cdot}1758 = \Delta$	—	—

A number of such experiments have been made and the value of the 'apparent velocity constant' plotted as in Fig. 8. A fall in the value followed by a slight rise was always found, before the value finally fell to zero at the point where maximum colour is attained. These phases during the course of the formation of blue are typical of the reaction in sea water, in salt solution and in distilled water.

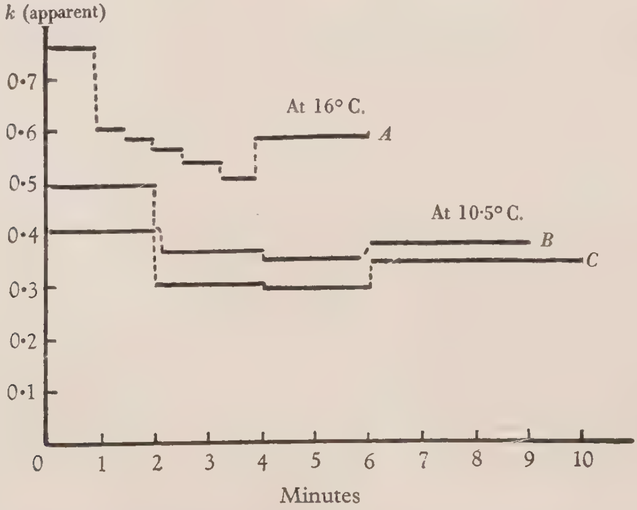

Fig. 8. The value of the apparent reaction velocity during intervals while blue was being formed in phosphate-enriched sea water. *A* at 16° C. and $6{\cdot}3\times10^{-5}$ M-Sn$^{\cdot\cdot}$; *B* at 10·5° C. with $8{\cdot}1\times10^{-5}$ M-Sn$^{\cdot\cdot}$; C at 10·5° C. with $2{\cdot}4\times10^{-5}$ M-Sn$^{\cdot\cdot}$.

The addition of a protective colloid hinders the aggregation of the electronegative blue micelles, thereby increasing the rate of colour formation. Gelatin, electropositive at this acidity, proved more potent than arabic. Both substances have a secondary effect, reducing the total colour developed possibly because they form complexes with the molybdic acid. Citric, oxalic

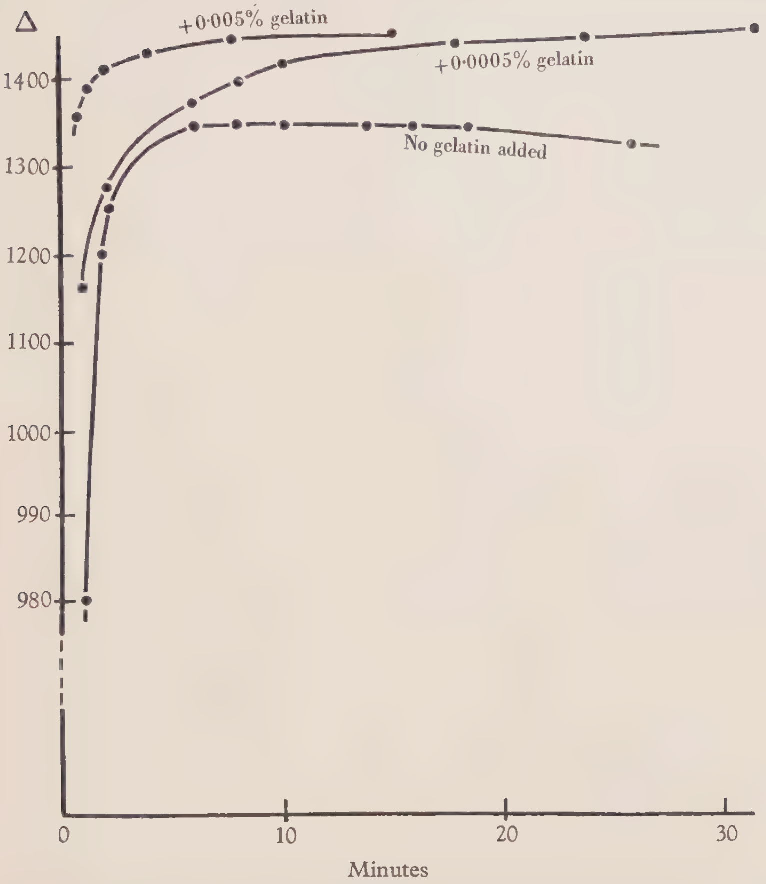

Fig. 9. The effect of a protective colloid on the formation of blue in a phosphate-enriched sea water.

TABLE I. INFLUENCE OF GELATIN ON THE APPARENT VELOCITY CONSTANT IN SEA WATER AT 16° C.

No addition		With addition of gelatin	
Interval (min.)	*k* (apparent)	Interval (min.)	*k* (apparent)
0 –0·92	1·4	0 –0·90	1·75
0·92–1·28	1·2	—	—
1·28–1·75	0·9	0·90– 2	0·334
1·75–2·15	0·44	—	—
2·15–4	1·0	2 – 4	0·260
4 –6	0·6	4 – 6	0·194
		6 – 8	0·174
		8 –12	0·10
		12 –24	0·11

Maximum colour reached in 10 min.

Maximum colour reached in 30 min

and other organic acids behave in this manner (Kalle, 1935; Berenblum & Chain, 1938; Tischer, 1934). Fig. 9 shows the effect of gelatin upon the reaction, and Table I shows its effect upon the 'apparent velocity constant', which no longer resembles that of a monomolecular reaction.

Different batches of reagent. Several batches of acid molybdate reagent have been used, and the increment in blue formed due to the addition of the same quantity of phosphate to sea waters determined. In Fig. 10 the increment in colour in terms of Δ or $E_{\text{cm.}}/7{\cdot}5$ is shown for an increase of 1 mg. phosphate-P per cm.^{3} as found on a number of occasions. This *increment value* appears to be almost constant, when the same quantity of stannous chloride has been used, and provided that the effect of temperature is taken into consideration—an increase of 1·2% per rise of 1° C. The line in the diagram is drawn to show this temperature relation.

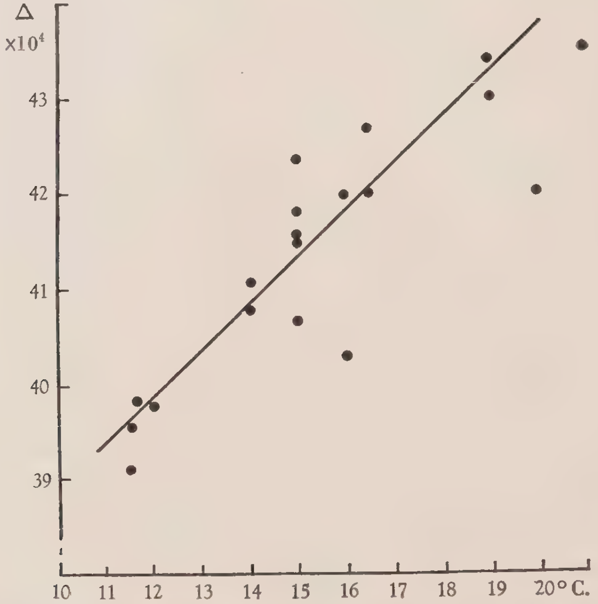

Fig. 10. The points show the increment in Δ due to the addition of 1 mg. phosphate-P per m.^{3}, obtained with different batches of reagent and different sea waters on different dates. The line shows the temperature relation as found by Kalle, being an increase of 1·2% per degree rise in temperature. The quantity of stannous chloride added varied between 0·35 and 0·44 mg. $Sn^{\cdot\cdot}$ to 67 c.c. of sea water plus 3 c.c. of reagents.

Since it has been noticed that the rate of colour formation and fading, at the same temperature, etc., differs slightly between one sea water and another, and since particles in suspension affect the colour formation, a precise agreement would not be expected. The majority of the values lie within about ±2% of the expected, which is greater than the probable experimental error.

Hence there appears some reason to suppose that sea waters may be met with which contain a substance which slightly inhibits the formation of blue.

Linear relation between phosphate present and colour formed. A number of experiments have been made which show proportionality. The following series of observations is illustrative:

	Δ observed	mg. P per m.^{3} calculated*	Increase
With distilled water	0·0032		
	0·0032		
	0·0024	Reagent-blank = 0·003Δ	
With filtered sea water	0·0120	2·20	
	0·0115	2·09	
Do. + 5 mg. phosphate P per m.^{3}	0·0320	7·1	5·1
	0·0335	7·5	5·4
Do. + 10 mg. phosphate P per m.^{3}	0·0535	12·4	10·3
	0·0533	12·3	10·2
Do. + 15 mg. phosphate P per m.^{3}	0·0735	17·2	15·1
	0·0735	17·2	15·1
Do. + 20 mg. phosphate P per m.^{3}	0·0910	21·6	19·5
	0·0900	21·5	19·3
	0·0905	21·4	19·3

* Being Δ observed less the reagent-blank, divided by the increment value for the temperature of the experiment, 14° C., this increment value being 0·00408Δ per mg. P per m.^{3}.

Successive reactions. If, after adding the stannous chloride and allowing the colour to develop fully, phosphate (in 0·28 N-H_2SO_4) is added within the next few minutes there is a second development of blue. The amount formed in this second reaction is slightly less than the increment due to adding the same quantity of phosphate initially. This lesser formation of colour appears due to some of the stannous chloride having been oxidized during the first reaction.

However, if, at the same time as adding the phosphate, a second addition of stannous chloride is made (about two-thirds of the quantity originally added) the amount of blue which develops is nearly equal to the increment when the same amount of phosphate is added initially. For instance:

Using filtered sea water at 18° C., the following readings were obtained on the photoelectric meter.

	log cm. virtual distance lamp to photocell	
	Sample A	Sample B
67 c.c. sea water + acid molybdate + Sn	1·8465	1·8470
After adding 20 mg. phosphate-P per m.^{3} and more Sn	1·7590	1·7600
Increment due to addition	0·0875	0·0870
After adding a further 20 mg. phosphate-P per m.^{3} and more Sn	1·6740	1·6760
Increment due to addition	0·0850	0·0840
67 c.c. sea water + 20 mg. phosphate-P per m.^{3} + acid molybdate and Sn	1·7620	1·7610
Increment over mean value of 1·8467 for water without added phosphate	0·0847	0·0857

Procedure adopted. (1) To 67 c.c. samples of sea water in 100 c.c. flasks were added 3 c.c. of an acid molybdate solution made by dissolving 6·5 g. of ammonium molybdate in 500 c.c. of water and 110 c.c. of concentrated sulphuric acid. This acid molybdate solution attains ionic equilibrium within 48 hr. and thereafter undergoes little or no change when stored in hard glass, but changes in contact with ground glass. It is equivalent to the Atkins-Denigès reagent diluted with an equal quantity of water. The addition is made most conveniently by means of a simple automatic pipette (Fig. 11) while swirling the sea water, in order to avoid the possible formation of chlormolybdate (*vide infra*).

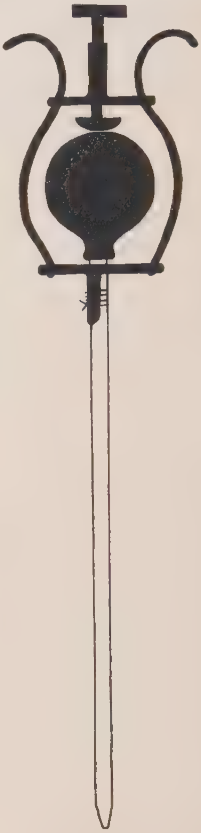

Fig. 11. Simple automatic pipette used for adding reagent while shaking contents of flask, showing rubber ball on glass pipette and plunger with limited travel adjusted to suck in and deliver the required quantity.

(2) The sea-water samples plus reagent are each transferred to the observation tube of the photoelectric meter, the d_0 readings obtained, and the liquids returned to the flasks.

(3) Three drops of a solution of stannous chloride in dilute hydrochloric acid, containing between 0·3 and 0·45 mg. $Sn^{\cdot\cdot}$, are then added while swirling each sample of the sea water plus reagent. Each sample is returned to the observation tube and the d_1 reading taken when the colour formation reaches a maximum. The time interval, after adding the reductant, during which 99·5% of the maximum colour is present, varies with temperature at

11° C.	14–23 min.
14° C.	12–18 min.
16° C.	11–15 min.
23° C.	5–14 min.

The difference between d_1 and d_0 or Δ is thus obtained for each sample, and the temperature noted. Before calculating the phosphate content it is necessary to subtract the value for the reagent-blank.

(4) The observation tube is very thoroughly washed to rid it of any trace of stannous ions, and the operations repeated using the same reagent and stannous chloride solution with distilled water. With distilled water the time interval after adding reductant during which 99·5% of the maximum colour is present is longer than with sea water at

9° C.	45–145 min.
15° C.	15– 45 min.
20° C.	10– 30 min.

The value found for Δ for each sample of sea water minus the value of Δ for distilled water (the reagent-blank) is then directly proportional to the phosphate content of the sea-water sample.

(5) The increment value for unit addition of phosphate-P per m.^{3} may be found by enriching samples with 20 mg. phosphate-P per m.^{3}. This is conveniently done by adding 0·3 c.c. of a solution containing 4·5 mg. phosphate-P per l. of 0·28 N-H_2SO_4 to 67 c.c. samples of filtered sea water by means of a Krogh syringe pipette.

Alternatively, the increment may be determined by adding phosphate and additional reductant after the d_1 reading has been obtained (p. 351).

The values of phosphate content obtained by the phosphomolybdate method of estimation include any *arsenate* which may be present in the water. Rakestraw & Lutz (1933) found between 7 and 24 mg. As per $m.^3$ in various samples of sea water, and if all this were present as arsenate it would cause the formation of blue colour equivalent to 3–10 mg. phosphate-P per $m.^3$. That at least some of the arsenic present in natural sea waters is in the form of arsenate seems probable, because if small quantities of sodium arsenite (20–40 mg. As per $m.^3$) are added to sea water it oxidizes to arsenate, the rate of oxidation varying between one sea water and another.

The values of phosphate found also include any particles of inorganic phosphate suspended in the water which dissolve in the 0·28 N-acid. Turbid inshore waters may contain considerable quantities. Thus a water collected off the Suffolk coast after filtration and addition of the acid reagent was found to contain 3·7 mg. phosphate-P per $m.^3$; but, when the acid reagent was added before filtering, 10·5 mg. per $m.^3$ were found. In the clear transparent waters of the English Channel, Cooper (1948) finds evidence of particulate phosphate in suspension varying hand in hand with the quantity of particulate iron present.

In consequence, it is to be expected that subsamples from the same sea water may vary in their phosphate content. In clear waters from the English Channel variations exceeding ± 1 mg. phosphate-P per $m.^3$ appear to be rare.

With subsamples of a filtered water, on the other hand, the variation appears to lie within or almost within the instrumental error, ± 0·25 mg. P per $m.^3$.

THE ESTIMATION OF ORGANIC PHOSPHORUS COMPOUNDS IN SOLUTION

Several attempts to estimate the total phosphorus in sea-water samples culminated in the successful methods devised by Kalle (1935) and by Redfield, Smith & Ketchum (1937).

The present investigation aimed at modifying this latter method to obtain a quicker and simpler technique. For survey purposes it had the disadvantage that the estimation involves several processes taking time; it also involved subtracting rather high and variable reagent blank-values.

Preliminary experiments, using visual colorimetry, showed that autoclaving at 135–140° C. for 5–6 hr. in 0·28 N-H_2SO_4 completely hydrolysed such compounds as nucleic acid, phospho- or glyceroproteins dissolved in sea water. It also completely hydrolysed the phosphoric esters in diatoms.

In control experiments using distilled water instead of sea water, the reagent-blank values were high and variable. It became apparent that phosphate leached out of the glass flasks into the 0·28 N-acid during autoclaving at 140° C., even after the flasks had previously been cleansed by heating in concentrated sulphuric acid. Finally, 100 c.c. silica flasks were used. These give consistent reagent-blank values equal to the values obtained without autoclaving.

During the cooking any arsenite was oxidized to arsenate; by adding a small quantity of sodium sulphite before heating, this was not only prevented but added arsenate was almost completely reduced to arsenite. These latter observations were confirmed after the method of phosphate estimation had been more fully developed.

Experiment showing the effect of adding arsenate to an aged and filtered sea water. Samples of the water, with and without the addition of 44 mg. arsenate-As per m.^{3}, were acidified to 0·28 N with sulphuric and 0·15 % $Na_2SO_3.7H_2O$ added. After autoclaving for 5 hr. at 140° C. and cooling, the volumes were made up to the original volumes and an acid molybdate solution added to give 0·05 % ammonium molybdate.

	Phosphate found mg. P per m.^{3}
Water only	7·6, 6·7, 6·7
Water and arsenate	7·0, 6·9

The photoelectric estimation of molybdenum blue allowed determinations to be made in water turbid with bacteria. This, in turn, allowed the question whether hydrolysis of the organic phosphorus was complete to be attacked by another and more exact method.

When sea water is enriched with asparagine (20 mg. per l.) and the bacteria allowed to proliferate, the inorganic phosphate is used up by the bacteria, which are singularly rich in phosphorus, having a C/P ratio of about 22. When phosphate was added to such a slightly turbid water and then estimated, the increase in phosphate due to this addition found by experiment was 4 % less than when the same quantity of phosphate was added to a control in which bacteria had not developed. Following this preliminary experiment a sea water containing 14½ mg. inorganic phosphate per m.^{3} was enriched with asparagine. Ten silica flasks were charged with this, five being incubated until all the dissolved phosphate had been used by bacteria while the other five were acidified and stored in the cold. Then, after hydrolysis at 140° C., the resulting phosphate (including the equivalent of any arsenic present) was estimated (Table II).

TABLE II. PHOSPHATE, IN MG. P PER M.^{3}, FOUND IN FLASKS

After storage without development of bacteria	After incubation and utilization of 14·5 mg. P per m.^{3} of dissolved phosphate by bacteria
22·6	21·6
22·75	21·7
22·2	21·0
22·4	21·2
22·6	21·6
Mean 22·51 ± 0·149	Mean 21·42 ± 0·165 + 4 % = 22·28 ± 0·172

Hence at least 93 % of the phosphorus in the bacterial tissue had been reconverted to phosphate in solution. Assuming that the bacterial cells, after cooking, reduced the colour formation by 4 % as they did in the previous experiment, virtually all the phosphorus in the bacterial tissue was reconverted to phosphate.

In the earlier experiments it was found that the use of ammonium molybdate solutions in distilled water led to high reagent-blank values; furthermore some anomalous results were obtained. This necessitated a study of the inter-ionic changes which take place in solutions of ammonium molybdate during storage and on their mixing with acidified sea water. The following observations were made.

Formation of silicomolybdate. On storing aqueous solutions of ammonium molybdate in glass bottles, their use resulted in high reagent-blank values, less so if the molybdate was dissolved in dilute sulphuric acid, and not at all if dissolved in 3 N or 6 N-acid.

No such progressive increase in the reagent-blank values resulted from the use of a 1·65 % solution of ammonium molybdate in 0·56 N-H_2SO_4 stored in waxed bottles.

Presumably silicomolybdate ions were formed during storage in glass and these were reduced to silicomolybdate blue by stannous chloride. The reduction takes place more rapidly than that of phosphomolybdate; another difference is that the same amount of blue is formed in sea water as in distilled water. In consequence the 'reagent-blank' resulting from the presence of silicomolybdate is not subject to salt error.

Experiment. A 1·65 % solution of ammonium molybdate in 0·56 N-H_2SO_4 was used which had been stored in a glass bottle for 2 months, its reagent-blank having meanwhile risen to a high value while the liquid had acquired a faint yellow tint.

With filtered sea water the blue formed after adding stannous chloride was the same, whether the reductant was added a few minutes or 18 hr. after the molybdate solution. This showed that the silicomolybdate ions were stable in sea water containing acid and molybdate at the customary concentration and acidity. The silicomolybdate blue developed more rapidly (80 % within 50 sec. at 10° C.) than the phosphomolybdate blue develops from the reduction of phosphomolybdic acid at the same temperature (80 % in *c.* 4·5 min.) and its subsequent rate of decay was less.

A further experiment was made with the same stored reagent in order to find whether the presence of a large quantity of silicomolybdate ions would interfere with the estimation of phosphate.

A filtered sea water was found to contain 7·0 mg. phosphate-P per m.^{3}, using a reagent with very low reagent-blank. The following estimation was then made using the glass-stored acid molybdate solution.

	Colour developed	
With distilled water (duplicate)	118·1 117·9	reagent-blank
With filtered sea water (duplicate)	145·2 144·8	
With same + 20 mg. phosphate-P per m.^{3}	222 222	

Increase in colour due to addition of 20 mg. P/m.^{3} = 77·0
Colour developed in filtered sea water (145) less reagent-blank (118) = 27·0

Phosphate content of filtered sea water $= \dfrac{27{\cdot}0 \times 20}{77{\cdot}0}$ or 6·8 mg. phosphate-P per m.^{3}

Silicomolybdate ions are formed on addition of a silicate to a relatively strong (1·65%) solution of ammonium molybdate in water or dilute sulphuric acid, but they are not formed if small quantities of silicate are added to 0·05% molybdate in 0·28 N-H_2SO_4. Thus they are not formed at room temperature *subsequent* to the addition of the molybdate reagent in phosphate determinations.

Some evidence was obtained of the formation of silicomolybdate while a 5% solution of ammonium molybdate mixes slowly with the acidified sea water, but not if a 1·65% solution in dilute sulphuric is used.

Formation of chlormolybdate. Evidence was obtained suggesting that within a limited range of acid and of molybdate concentration chloromolybdic ions may be formed in the presence of chloride. The supposed chloromolybdate is reduced by stannous chloride to a blue; the chlormolybdate is unstable at greater dilution in sea water made 0·28 N with sulphuric acid, slowly reverting to molybdate. The above conclusions rest on the following observation.

(*a*) When sulphuric acid was added to sea water without shaking, so that the upper levels in the flask were less acid, and molybdate then added, the flask being later shaken before adding reductant, over twice as much blue colour developed than when the water and acid had been thoroughly mixed prior to the addition of the molybdate.

(*b*) A solution was made containing 1·67% ammonium molybdate and 3½% sodium chloride in 0·28 N-sulphuric acid. After it had stood for 4 days, its addition to acidified sea water in the customary proportions followed 15 min. later by stannous chloride led to the formation of a strong blue colour. If the reductant was added 30 min. after the acid-salt-molybdate solution, the blue colour formed was 25% less. The experiment suggested that chlormolybdate ions had formed in the acid-salt-molybdate solution, and on adding this to sea water made 0·28 N with sulphuric acid, these ions slowly reverted.

The foregoing observations led to the adoption of the following procedure in estimating the total phosphorus in a water sample—phosphorus present as phosphate in solution, as organic phosphoric esters in solution, in microplankton and in organic detritus, and as phosphate present as inorganic phosphate particles.

Procedure adopted for estimation of total phosphorus in water samples. To 67 c.c. of sea water in 100 c.c. silica flasks are added (i) exactly 1 c.c. of concentrated sulphuric acid which has been diluted with an equal volume of water, (ii) 4 drops of a saturated solution of sodium sulphite. The flasks are then covered and heated for 5–6 hr. in a pressure cooker at between 30 and 40 lb. per sq.in. After cooling the volume of each is made up to 68 c.c. with distilled water, the contents being thoroughly mixed. Then, while the contents are being swirled in the flask, 2 c.c. of a solution containing 6·6 g. of ammonium molybdate in 400 c.c. of water plus 6 c.c. of concentrated sulphuric acid are added. This addition is conveniently made by means of an automatic pipette (Fig. 11); the use of a burette or any contact with ground glass is to be avoided. The molybdate solution is stored in a waxed bottle, and appears to attain interionic equilibrium within 48 hr. after being made.

The d_0 and d readings are taken. From the Δ values so obtained the phosphate contents are calculated after subtracting the reagent-blank.

These values are subject to a small, almost insignificant, correction because the acidity is reduced by about 4% as the sulphur dioxide formed is driven off during cooking. This reduction in acidity causes 2% more colour to be formed: therefore the calculated values of phosphate content are subject to a correction of −2%.

The estimations of phosphate by this (or Redfield's) method will not include the equivalent of any arsenate present in the water.

Variable quantities of microplankton organisms and of particulate phosphate are likely to occur in subsamples of the same sea water. Some data showing the variability encountered in offshore English Channel waters are given in the following.

(i) Sea water collected near the Eddystone Lighthouse, 30 September 1946, at a depth of 2 m., contained an appreciable quantity of particulate matter. Estimation of phosphate in seven subsamples showed the presence of 12·0, 12·6, 12·6, 12·6, 12·7, 12·8, 12·8 mg. phosphate-P per $m.^3$.

Estimation of total phosphorus in seven subsamples showed the presence of 16·1, 16·1, 16·1, 16·5, 16·5, 17·0, 17·0 mg. P per $m.^3$.

(ii) Subsamples of raw sea water collected 10 miles south of the Eddystone at a depth of 2 m. on 5 December 1946 were found to contain 12·9, 12·9, 13·2, 13·4, 13·6, 14·0 mg. phosphate-P per $m.^3$, and 15·7, 17·3, 17·65 mg. total P per $m.^3$.

Storage of sea-water samples. Early in this investigation it was found that when sea water is stored in glass bottles, the quantity of total phosphorus in solution and suspended particles decreases. This might be expected, since there is a rapid development of bacteria firmly attached to the glass surface during storage in small vessels and since bacteria are singularly rich in phosphorus. However, when sea water, collected during the summer when the organic phosphorus in solution is at a maximum, was saturated with chloroform, which hinders but does not entirely stop bacterial growth, or was acidified (0·28 N) and stored for a few days, there was also a reduction in total phosphorus. A clean glass surface adsorbs organic matter when in contact with sea water (Harvey, 1941; ZoBell & Grant, 1943), and presumably some organic phosphorus is lost by adsorption during storage. I am indebted to Dr J. F. Danielli for the information that a glass surface may adsorb a layer, some 50 Å. thick, of certain proteins or nucleic acids. This suggests that storage in small glass vessels could reduce the concentration of organic matter in solution materially.

It was therefore essential to find some method of storing samples without loss of organic phosphorus by attachment to the storage bottle. Experiment indicated, as far as the methods of estimation permitted, that this can be done by means of a simple device. Before filling with a measured quantity of sea water, the storage bottles were 'baited' with a small quantity of recently precipitated aluminium hydroxide, in order that the adsorbable organic matter and any epiphytic bacteria might attach to the large surface exposed by this finely divided and reactive solid rather than to the glass, and a few drops of chloroform were also added to hinder the proliferation of bacteria. After storage the sulphuric acid was added to the storage bottle; this quickly dissolved the alumina, unseating the adsorbed organic matter and attached bacteria. The whole contents of the bottle were then poured into the silica reaction flask.

Later a suspension of thorium carbonate was substituted for aluminium hydroxide as bait, because the latter becomes less rapidly soluble in sulphuric acid after more than a week or 10 days' storage.

Water collected 22 July 1946 near Eddystone Lighthouse, was found to contain:
Filled direct into flasks: 14·0 mg. P per m.^{3} (mean of 4 estimations).
After storage in glass bottles: 10·5 mg. P per m.^{3} (mean of 4 estimations).
After storage in 'baited' bottles: 14·7 mg. P per m.^{3} (mean of 4 estimations).

Water collected 17 August 1946 near Eddystone Lighthouse:
Filled direct into flasks: 16·3 mg. P per m.^{3} (mean of 6 estimations).
After storage in baited bottles: 16·9 mg. P per m.^{3} (mean of 8 estimations).

Water collected off Eddystone Lighthouse 17 September 1947:
Filled direct into silica flasks: 17·0, 16·7, 16·4, 15·7, 15·4, 15·0, 14·8, 14·7, 14·2 mg. P/m.^{3} (mean 15·54).
Stored 4 days in bottles baited with thorium carbonate: 17·8, 16·1, 15·6, 15·6, 14·8 mg. P/m.^{3} (mean 16·0).
Stored 4 days in glass bottles in dark: 16·4, 13·9, 13·6, 13·6, 12·7 mg. P/m.^{3} (mean 14·0).

Results obtained by using this technique, with the object of investigating the cycle of phosphorus in the sea, its changes with time, depth and place, will be the subject of a further communication. Yet it seems desirable to include a series of data, typical of several such, from clear offshore water of moderate depth in summer (Table III).

TABLE III. PHOSPHORUS IN OFFSHORE WATER

Position, 3 miles south of Eddystone Lighthouse. Depth, 67 m. 23 July 1947.

	mg. P per m.^{3}		
Depth in m.	Inorganic*	Total	Organic†
5	2·3	10·2	7·9
10	2·2	11·6	9·4
20	5·0	12·3	7·3
30	6·5	12·6	6·1
40	7·4	11·8	4·4
60	6·8	13·1	4·3
65	6·8	14·2	7·4
35 cm. above sea floor	8·4	14·7	6·3
6 cm. above sea floor	8·8	24·0	16·2
6 cm. above sea floor (200 yd. distant)	7·9	18·0	10·1

* Including the equivalent of any arsenate present. † By difference.

I would wish to acknowledge many most helpful conversations with Dr W. R. G. Atkins, F.R.S., and Dr L. H. N. Cooper, F.R.I.C., who also carried out a number of check estimations by means of a Pulfrich photometer during the early part of the investigation.

SUMMARY

A simple photoelectric meter is described which allows the molybdenum blue formed in sea water, due to the presence of phosphate, to be estimated within that due to ±0·25 mg. phosphate-P per m.^{3}.

The effects of concentration of acid, molybdate, reductant, temperature and suspended particles on the rate of formation, fading and amount of molybdenum blue, formed in sea waters containing phosphate are detailed.

Intramolecular changes taking place during storage of molybdate solutions, and while being mixed with acidified sea water, have been investigated.

The hydrolysis of organic phosphorus compounds in acidified sea water at 140° C., and the prevention of arsenate formation, are described.

Procedures, resulting from these investigations, for the estimation of phosphate, and of total phosphorus, are described.

The growth of bacteria and the physical adsorption of organic phosphorus compounds in solution on the walls of glass vessels used for storage of sea water have been investigated, and a method of prevention evolved.

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FURTHER EXPERIMENTS ON THE FERTILIZATION OF A SEA LOCH (LOCH CRAIGLIN). THE EFFECT OF DIFFERENT PLANT NUTRIENTS ON THE PHYTOPLANKTON

By S. M. Marshall, D.Sc. and A. P. Orr, M.A., D.Sc.

From the Marine Station, Millport

(Text-figs. 1–10)

Introduction

In 1942 and 1943 an experiment was made on the effect of adding nutrient salts to an isolated body of sea water. The experiment, which was initiated by Dr F. Gross of Edinburgh University and financed by Imperial Chemical Industries, Billingham Division, was carried out in Loch Craiglin, a small salt-water loch about eighteen acres in area and 70,000 m.^{3} in volume opening off one of the arms of Loch Sween on the west coast of Argyll. It is connected with Loch Sween by a narrow channel and the entrance and exit of water could be partly controlled by a dam. Loch Craiglin (Fig. 1) is shallow, most of it being less than 2 m. in depth, although there is a small area up to 5 m. deep opposite the mouth of the channel. The bottom is mostly soft mud but round the edge there are patches of sand or sandy mud. A small burn enters at the north-eastern end.

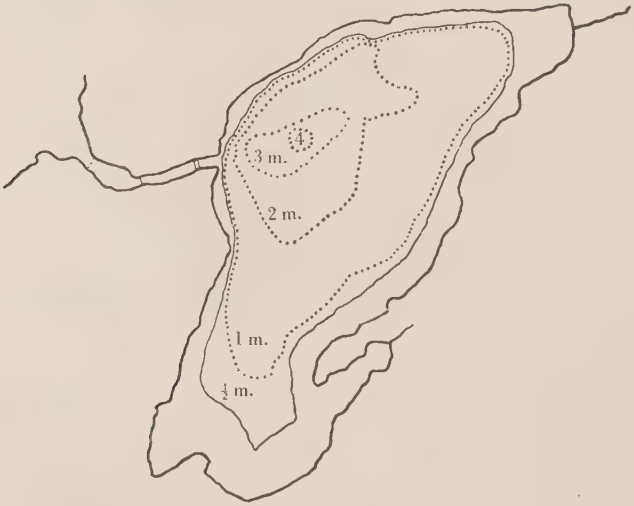

Fig. 1. Sketch-map of Loch Craiglin showing approximate depth contours. Scale 15 cm. = 1000 m.

The plankton and hydrographic results from the first two years' work have already been described (Marshall, 1947; Orr, 1947) and it was shown that the addition of nutrients sometimes caused an immediate increase in the phytoplankton. In the early work the effect of the nutrients was assessed during visits made at about fortnightly intervals. The present paper deals mainly with a series of experiments in which the effect of added nutrients, both on the phytoplankton and on the hydrographic conditions, was followed from day to day.

We should like to express our thanks to Imperial Chemical Industries for their support, and also to our colleagues Dr F. Gross, Prof. J. E. G. Raymont, Dr D. T. Gauld and Mr S. R. Nutman for help in taking samples.

METHODS

The methods of chemical analysis and for sampling the plankton were the same as those described in the earlier papers.

There was considerable interference with the accuracy of the estimations of phosphorus and nitrogen compounds, both because of the richness in phytoplankton organisms and the presence of free sulphide in the deep water. To avoid damage to the glass electrode pH readings were not taken at 3 m. when hydrogen sulphide was present.

During the fertilization experiments the number of μ-flagellates in all water samples was counted daily on a haemocytometer slide without concentration. However, the fluctuations from day to day were so great that although some of the increases in numbers may be related to fertilizations, others were not and it is felt that a further study of the methods of counting and of the normal seasonal and diurnal variations in numbers is needed before any conclusions can be drawn. The numbers were, however, high when compared with counts from elsewhere, varying from a few hundred to several thousand per $mm.^3$

Pump samples were taken on each visit in 1944 and once during each fertilization in 1945. The zooplankton on the whole was rather poor except for rotifers, and as might be expected showed no direct relation to fertilization. *Oithona* (chiefly *O. nana*) was the most abundant of the copepods.

Fertilizers were distributed by mixing up the solids with a large excess of loch water in a rowing boat and baling out the supernatant liquid into the loch. This was repeated until all had been distributed. It was spread as evenly as possible by rowing across the loch in a series of parallel lines while baling, but owing to wind and weather it was not always possible to keep accurate lines. Most of the nitrogen compounds dissolved readily but the superphosphate was not easily soluble and some of it certainly went to the bottom as solid.

FERTILIZATION EXPERIMENTS

During the whole of the autumn and winter of 1943–44 the loch was rich in phytoplankton, mainly dinoflagellate, although there was a short outburst of diatom growth found on 26 November and 11 December. The dinoflagellate plankton consisted mainly of *Peridinium triquetra* and *Gymnodinium* spp., the diatoms of a minute form, *Chaetoceros simplex*, which Miss M. V. Lebour kindly identified.

The numbers of dinoflagellates continued to rise at the surface and at 1 m. throughout December 1943 and January 1944 (Figs. 2, 3). A fertilization was made on 18 January with the usual quantities of sodium nitrate (142 lb.) and superphosphate (44 lb.) which is sufficient to raise the nitrogen and phosphorus from zero to well above normal winter sea values. The plankton was not examined again until 31 January when diatoms (minute *Chaetoceros* sp.) were very abundant and dinoflagellates had increased once more. They were almost entirely *Peridinium triquetra* and at the surface had reached a figure of 2350 per ml.

By 9 February diatoms had almost disappeared but dinoflagellates were still increasing. *P. triquetra* now numbered 3500 per ml. at 0 and 1 m. and 1125 per ml. at 2 m. A fertilization was made on 11 February using nearly three times the usual quantities of sodium nitrate (336 lb.) and superphosphate (112 lb.) and the plankton was sampled on 19 February. The *P. triquetra* had increased to over 6000 per ml. at the surface and 1730 at 3 m. but diatoms were practically absent. Seventeen days later on 7 March, *P. triquetra* had reached its maximum in the surface layer, 8165 per ml., but was scarce in deeper water and diatoms were still absent.

To find the amount of photosynthesis going on, samples of the phytoplankton-rich surface water were suspended in bottles at different depths on 20 February with similar controls kept in the dark. In spite of the enormous numbers of dinoflagellates, however, the oxygen production in these bottles over 24 hr. was negligible at all depths.

The numbers of dinoflagellates remained high, over 1000 per ml., until the middle of June although the species present altered as time went on. On 9 April *Gymnodinium* spp. outnumbered *Peridinium triquetra*, though both were abundant. On 27 April this change had gone still further and *Gymnodinium* spp. had risen to 2435 per ml. at the surface, while *Peridinium triquetra* had declined to 130 per ml. *Gymnodinium* remained predominant in May and June but at the beginning of July dinoflagellates had decreased to figures of 30 or 40 per ml. At the end of June there was a sudden and short-lived increase in diatom numbers, again the minute *Chaetoceros* sp.

The number of 30 or 40 dinoflagellates per ml. would be considered very high in normal sea plankton; it is low only in comparison with the extraordinarily high figures throughout the winter and spring in Loch Craiglin. The

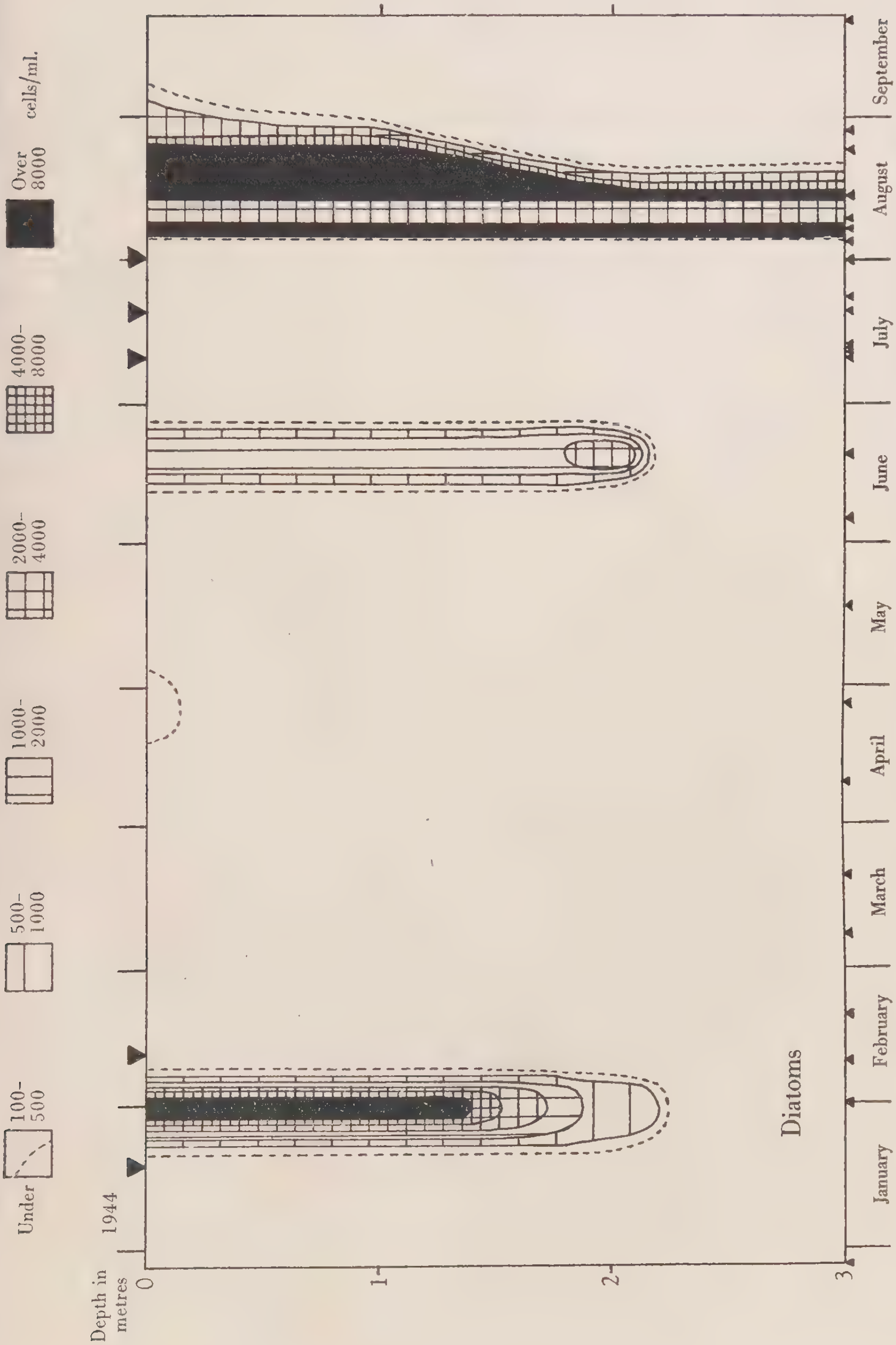

Fig. 2. Number of diatoms at Station I, Loch Craiglin, during 1944. Large triangles above show dates of fertilizations; small triangles below show dates of sampling.

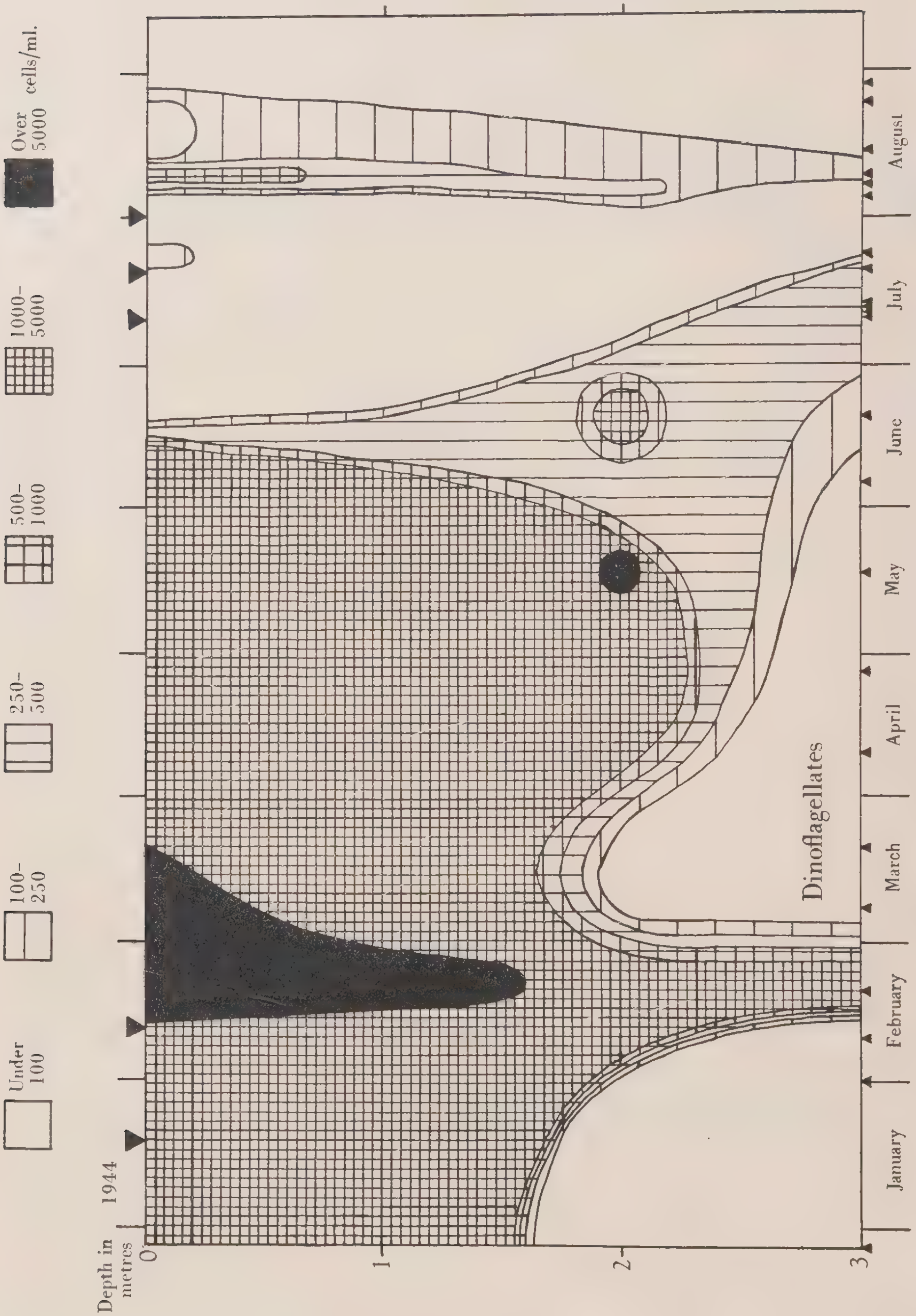

Fig. 3. Number of dinoflagellates at Station I, Loch Craiglin, during 1944.

most abundant species, *Peridinium triquetra*, usually has a summer maximum and it is a form which, under favourable conditions such as in the polluted waters of the inner Oslo Fjord (Braarud, 1945), is capable of increasing until it forms a 'waterbloom' or 'red water'. The maximum number recorded elsewhere, however, is a little below 3000 per ml.; in Loch Craiglin it rose to over 8000 per ml. on two occasions and remained above 2000 per ml. for weeks on end. The water in the loch had during this period a distinct brownish red tinge.

There are several interesting points about these winter fertilizations. The first of them, on 18 January, was followed by a great increase of diatoms but dinoflagellate numbers, very high already, showed no comparable increase. On the other hand, the second fertilization on 11 February was followed by a decided increase in dinoflagellate numbers but had no effect on diatoms although the fertilizer added was nearly three times the usual amount. As a general rule in the open sea dinoflagellates follow diatoms in their times of maximum abundance and they are said (Barker, 1935) to be able to use lower concentrations of nutrients than the former. It is therefore surprising to find an increase of diatoms (19 June) following immediately upon the dying away of dinoflagellates.

The plankton in Sailean More, the open arm of Loch Sween with which Loch Craiglin is connected, showed no comparable changes; dinoflagellates were scarce throughout and, although there was a great rise in diatom numbers in April (over 2000 per ml. at 1 m. on 27 April), the form was a *Leptocylindrus* sp. The minute *Chaetoceros* sp. so characteristic of Loch Craiglin did not appear in Sailean More.

A curious feature of the spring of 1944 in Loch Craiglin was that the phytoplankton remained rich throughout the spring months when, in other years, fertilizations at that time had little or no effect on the phytoplankton because the attached vegetation seemed to have first call on the nutrients.

In July and August a series of fertilizations was begun and each was followed up by sampling at short intervals, usually 1 or 2 days (Figs. 4–6). The first fertilization was made with superphosphate alone, the second with nitrate alone and the third with ten times the usual quantity of both.

During these months there was a rich vegetation, consisting partly of algae (chiefly *Enteromorpha* and *Cladophora*) and partly of *Zostera* and *Ruppia*, round the shores and this interfered considerably with the experiments.

On 10 July, 66 lb. superphosphate was added. This caused a rise in soluble phosphate chiefly at the surface which lasted for only 2 or 3 days. The pH and percentage oxygen saturation rose after the fertilization, in agreement with the utilization of the soluble phosphate, though the highest figure for oxygen (150% saturation) was at 1 m. At the surface equilibrium of oxygen with the air seems to be reached rapidly. Nitrate was present down to 2 m. and although it was only in small quantities it does not seem probable that it was a limiting factor.

This fertilization had no visible effect on the phytoplankton. Dinoflagellates were present in fair numbers but diatoms were absent. This suggests that

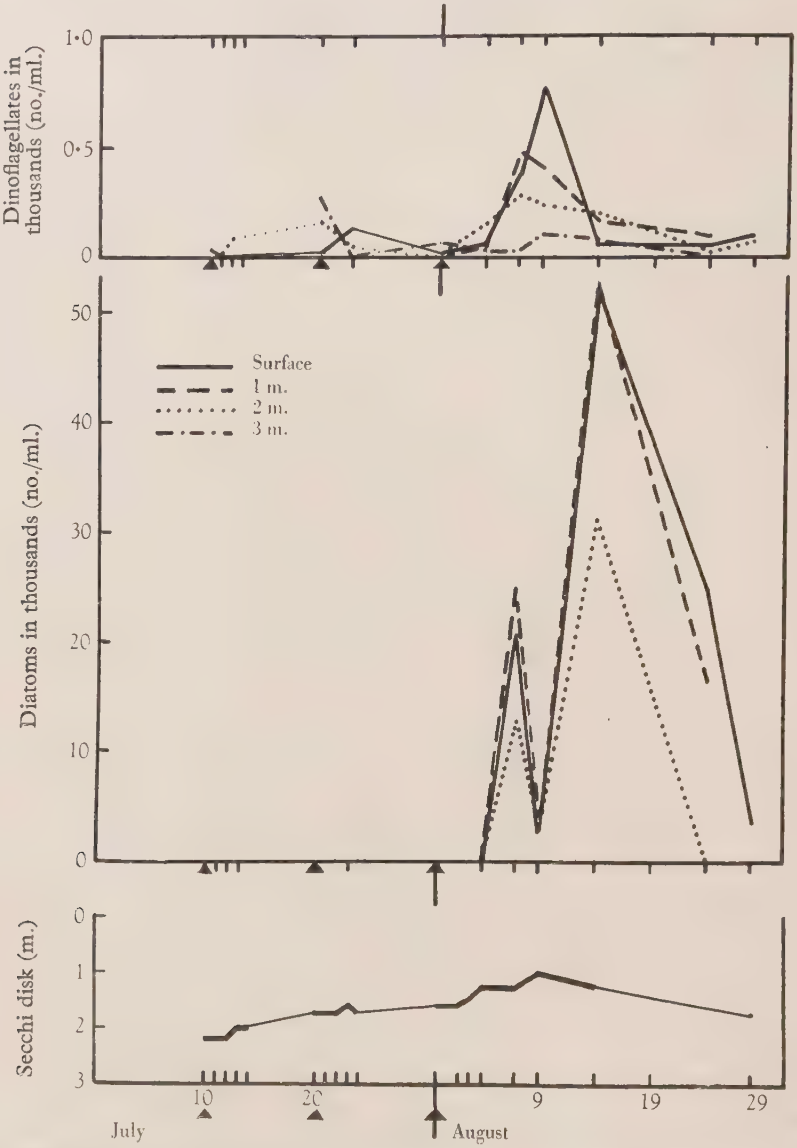

Fig. 4. Effect on the phytoplankton and the transparency of the water of fertilizations during July and August 1944. Triangles below show dates of fertilizations.

the vegetation round the shore and in shallow water was absorbing all the nutrients.

On 20 July, 141 lb. sodium nitrate was added. This caused a rise in nitrate-N at all depths. Values remained high for 3–4 days but after a week were back to normal. Percentage oxygen saturation and pH were high except in deep water; the values were affected by slight salinity changes caused by an influx of water from Sailean More.

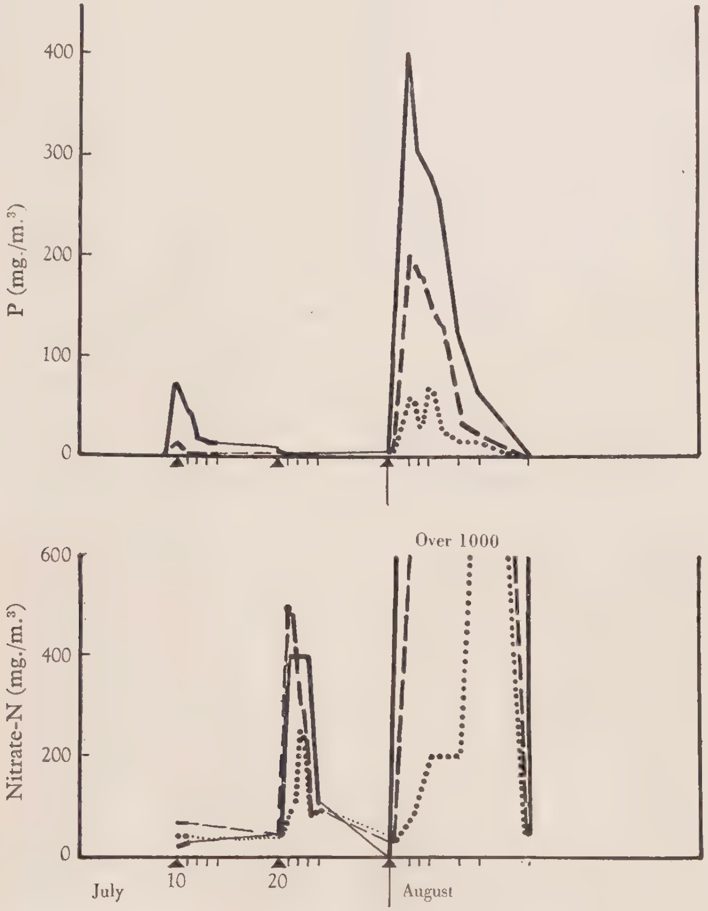

Fig. 5. Changes in nutrient salt concentrations during fertilizations in July and August 1944. Depths marked as in Fig. 4.

Although there was apparently a slight increase of dinoflagellates (naked forms, mainly *Gymnodinium* spp. and *Oxyrrhis marina*), this is probably not significant, since the numbers actually fell at 1 m. from 20 to 23 July.

The fertilization with about ten times the usual quantity of nutrients (1344 lb. sodium nitrate and 448 lb. superphosphate) was done on 1 August. This raised the dissolved phosphate up to 400 mg./m.³ at the surface and to high

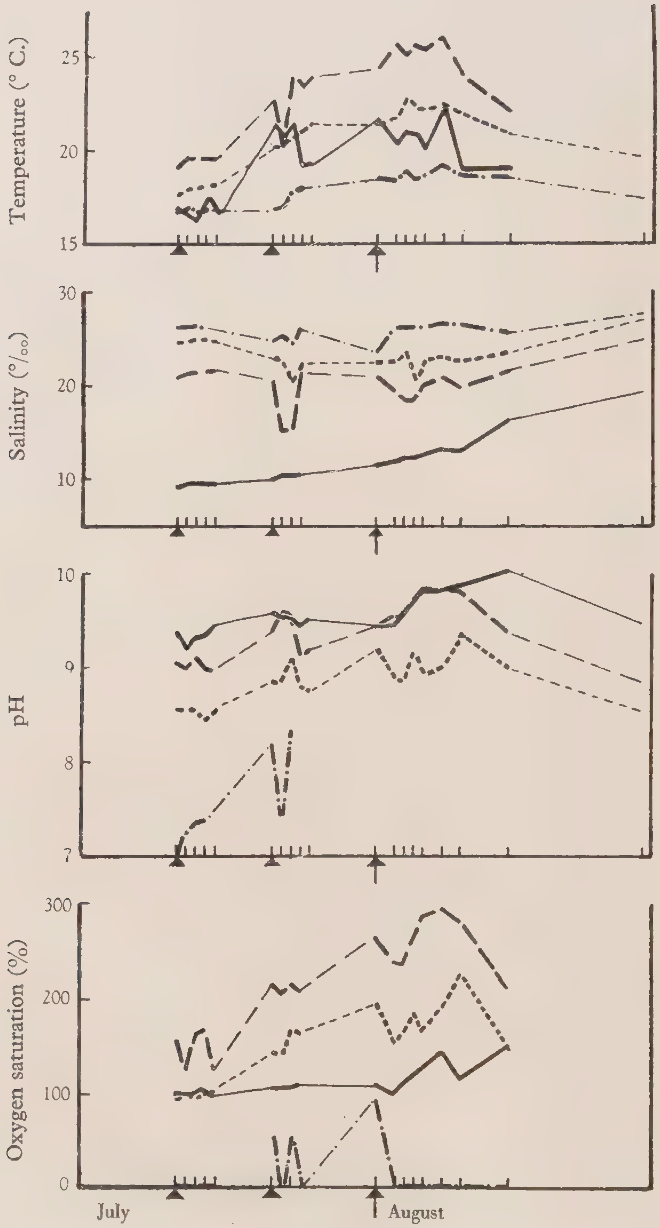

Fig. 6. Hydrographic and chemical changes during fertilizations in July and August 1944. Depths marked as in Fig. 4.

values in deeper water also. Utilization was rapid and in less than a fortnight values were back to normal. A rise in pH and percentage oxygen saturation coincided with the utilization of the soluble phosphate. Nitrate-N, very high immediately after fertilization, fell to normal within a fortnight.

Phytoplankton was very poor on the day of fertilization and for several days after, but on the seventh day after fertilization, diatoms were present in large numbers at all depths. There was a curious and unexplained fall in numbers (not confirmed by Secchi disk readings) on 9 August, but on the 14th the numbers were very high indeed (just over 50,000 cells/ml.) and thereafter fell rapidly. Three species took part in the increase, *Chaetoceros simplex*, a minute Naviculid and the triradiate form of *Nitzschia closterium*. Dinoflagellates also became abundant. Their numbers rose from 31 July to 4 August and again from the 4th to the 9th after which they fell. *Exuviella marina* was the commonest form, but *Gymnodinium* spp. also increased.

Compared with the first two fertilizations this one did produce a large increase in the phytoplankton, but only after a lapse of 4 days for dinoflagellates and of 7 days for diatoms.

The results of these three fertilizations suggest that only when the needs of the attached algae have been satisfied can the phytoplankton utilize any remaining nutrients. During the nitrate fertilization, however, the very low phosphate may have been a limiting factor. It is also possible that some of the nutrients are adsorbed by the mud or by non-living material suspended in the water. This would explain their very rapid disappearance.

The above experiments, as well as earlier work in this loch (Marshall, 1947; Orr, 1947), indicate that when shore-living algae are growing, fertilization does not result in an increase in phytoplankton except when very large quantities of nutrients are used.

During the winter the attached algae are absent or dormant but there is still enough light to permit photosynthesis in the shallow water of Loch Craiglin. A series of experiments was therefore carried out during the winter months to find whether other forms of inorganic phosphorus and nitrogen besides nitrate and superphosphate could be used by the phytoplankton (Figs. 7–9). The following combinations were tested:

(1) Superphosphate and sodium nitrate as normally.
(2) Superphosphate and ammonium sulphate.
(3) Superphosphate and ammonium nitrate.
(4) Mono-ammonium phosphate and ammonium sulphate.

The salts used were all available commercially as fertilizers, but were nevertheless of high quality.

Ammonium salts were chosen both because of the biological interest of testing whether ammonia-nitrogen could be used directly by the phytoplankton and because it is one of the commonest artificial fertilizers applied to land and so available in large quantities. Ammonium nitrate is used as an explosive and

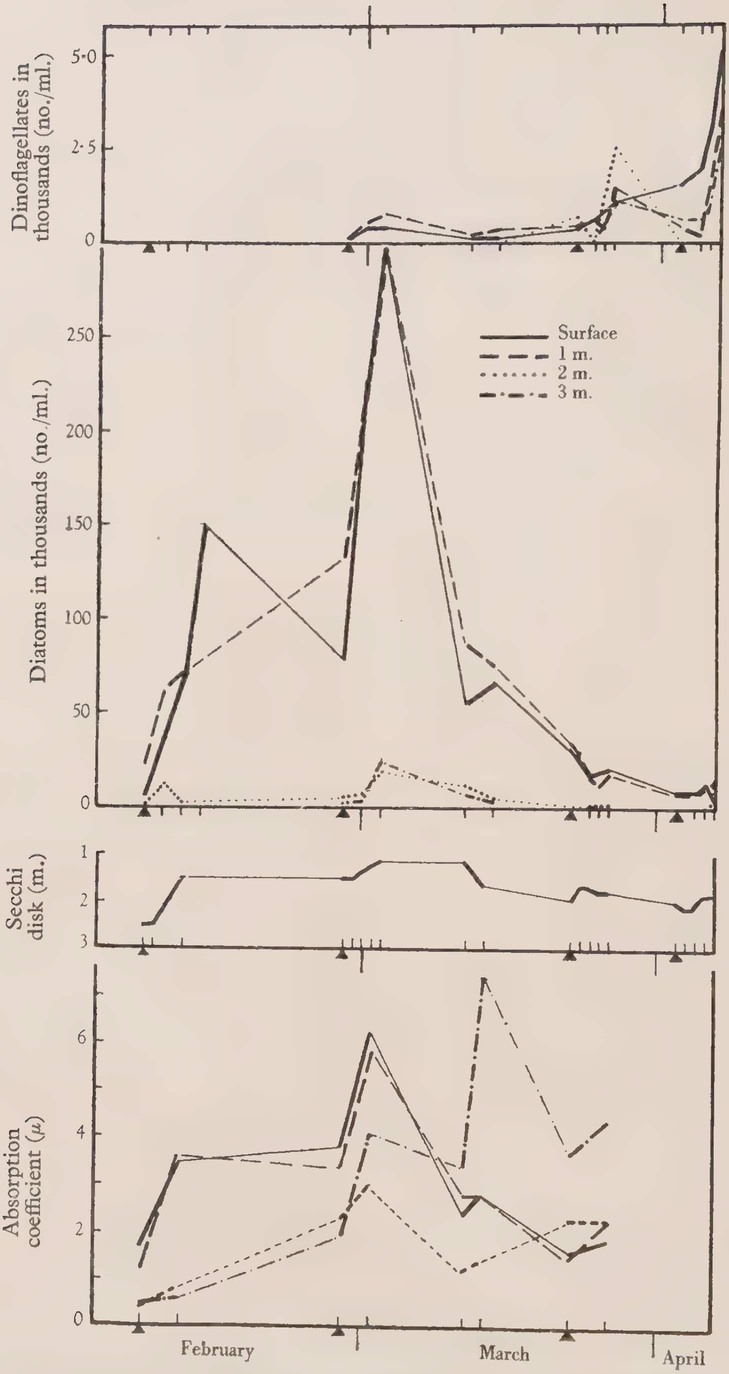

Fig. 7. Effect on the phytoplankton and the transparency of the water of fertilizations during February to April 1945.

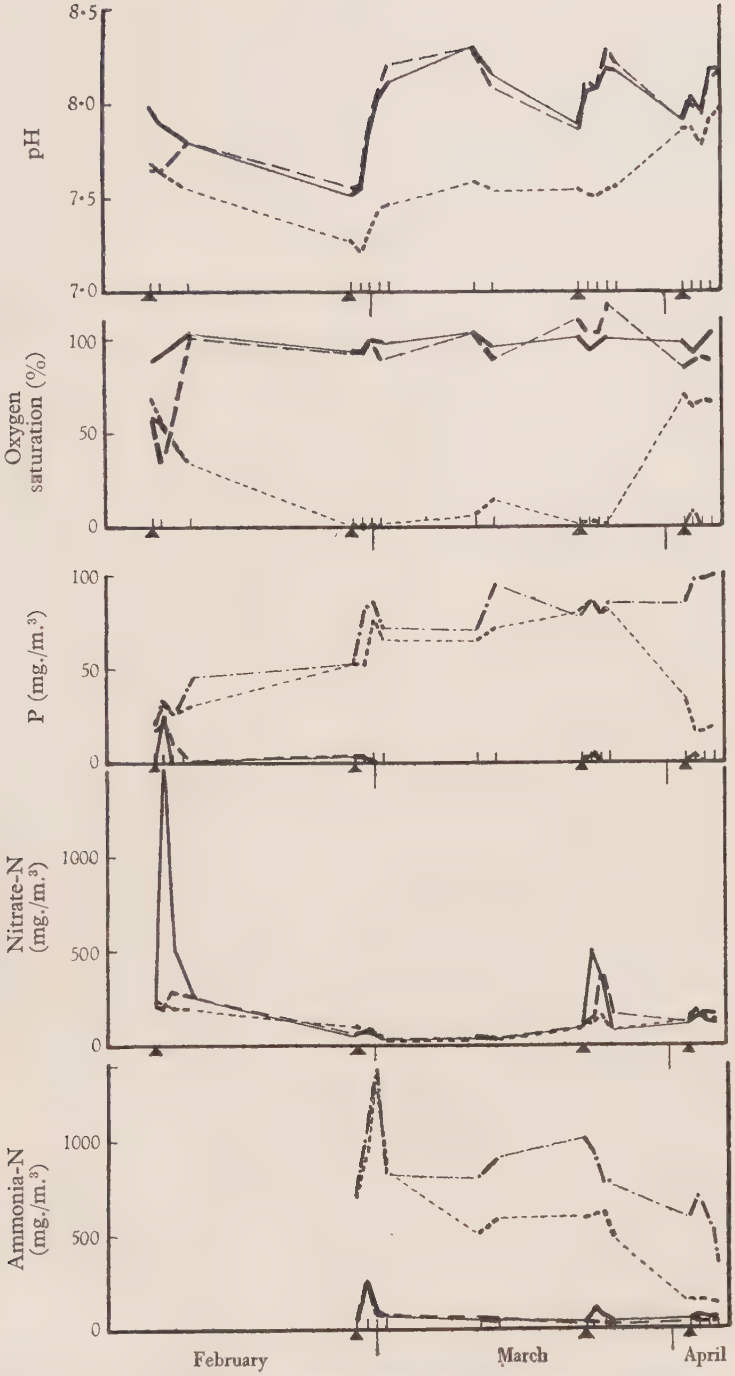

Fig. 8. Changes in nutrient salts and other chemical factors during fertilizations in February to April 1945. Depths marked as in Fig. 7.

might at times be available for disposal in considerable quantities. In addition it has a high percentage of nitrogen and would therefore be less expensive to transport. Mono-ammonium phosphate is much more readily soluble than superphosphate and also contains a much higher percentage of phosphorus quite apart from the ammonia-nitrogen present.

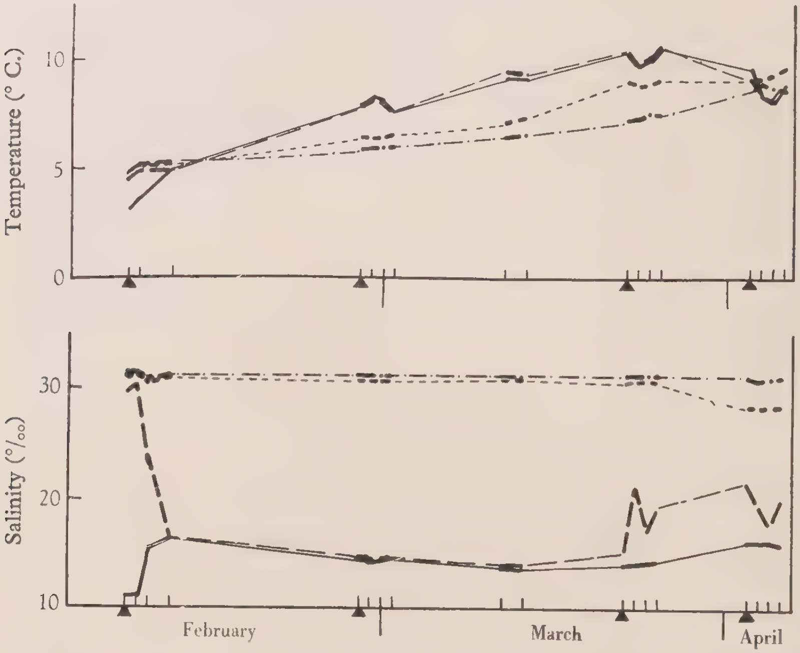

Fig. 9. Hydrographic changes during fertilizations in February to April 1945. Depths marked as in Fig. 7.

Each of them was tested on diatom cultures in the laboratory by Miss F. A. Stanbury of the Technical College, Plymouth, who used them as a source of nutrients in the following culture material:

(*a*) *Nitzschia closterium* pure.
(*b*) Almost pure *Achnanthes longipes*.
(*c*) *Amphipleura* sp.
(*d*) A mixture culture of (*a*), (*b*) and (*c*), with other forms.

None of them proved toxic even in relatively high concentrations (up to 25 mg./l.) and growth was as good as, or better than, that in controls in 'aged' or nutrient-enriched sea water. We are indebted to Miss Stanbury for carrying out these tests and for her permission to quote the results.

In each fertilization the same amount of phosphorus and nitrogen, namely 3·4 and 23 lb. respectively, was added to Loch Craiglin. This was roughly the same as in the normal fertilizations with sodium nitrate and superphosphate and was enough to raise the concentration to well above average winter sea values.

During the winter the dam was open to allow interchange with the main loch outside, and aeration of the deep water was fairly good. The dam was closed on 5 February 1945 and the normal amounts of fertilizers added that afternoon in the form of sodium nitrate and superphosphate. Phosphate was initially high at 1, 2 and 3 m. and after the fertilization rose at all depths. The day following fertilization, however, soluble phosphate dropped to zero at the surface and 3 days later was absent at 1 m. Nitrate gave winter values at the surface before fertilization and increased afterwards only at the surface. The following day it fell abruptly at the surface and 2 days later values were only slightly above normal winter concentrations.

During the course of the experiment changes in salinity showed that the surface and 1 m. layers had mixed. This affected the pH and percentage oxygen saturation values at these depths.

Diatoms (*Chaetoceros simplex*) were abundant in the loch before fertilization (5300 cells/ml. at the surface and 22,500 cells/ml. at 1 m.), and increased afterwards to 149,000 per ml. at the surface on the 11th. Dinoflagellates were scarce and showed no significant change. This enormous production affected the transparency of the water considerably. The Secchi disk which initially was visible down to 2½ m. was visible only to 1½ m. on the 9th. Measurements of the absorption coefficient with the Pulfrich absorptiometer showed a rise from 1·7 and 1·3 at 0 and 1 m. on the 5th to 3·5 and 3·7 on the 9th. In deeper water there was little change (Fig. 7).

On 26 February the loch was fertilized again with 42 lb. superphosphate and 110 lb. ammonium sulphate. In spite of this addition no phosphate appeared at the surface or 1 m. although there was a rise below this at 2 and 3 m. where the phosphate value had in any case remained high since the previous fertilization. This immediate disappearance of added nutrients was found on several occasions and is not understood. The rapidity suggests that absorption either by the phytoplankton and fixed algae, or else adsorption by dead particulate matter, is responsible.

The added ammonium sulphate did cause an increase, though a small one, in the ammonia present at the surface and 1 m. as well as a greater increase at 2 and 3 m. Nitrate remained low. All the nutrients had fallen to their original level in 2 days.

At no other time was a fertilization made when phytoplankton was initially so abundant. Although numbers had fallen at the surface from 11 February, they had risen at 1 m. and at both these depths were very high indeed (77,000 cells of *Chaetoceros simplex* per ml. at the surface and 133,000 at 1 m.). These high numbers rose still further on succeeding days; on 28 February there were over 200,000 and on 2 March nearly 300,000 cells/ml. down to 1 m. At 2 and 3 m. numbers were much lower (18,000 and 24,000 cells/ml. respectively).

Dinoflagellates were relatively unimportant but did show a slight increase. *Oxyrrhis marina* was the most abundant species.

Accompanying the great increase in diatoms there was a sharp rise in pH in the surface layers from 7·6 to 8·3, and there was a slight effect even at 2 m. The change, however, in percentage oxygen saturation was small. The transparency of the water, which was initially the same as at the end of the previous fertilization, showed an abrupt decrease, especially at the surface and 1 m. By 1 March the water was very turbid indeed, the absorption coefficient being 6·2 and 5·8 at 0 and 1 m. respectively.

The results of this fertilization confirm the findings in the laboratory of Harvey (1933) and ZoBell (1935) that ammonium salts can be used directly by the phytoplankton.

In Loch Craiglin (of which the greater part is less than 2 m. in depth) photosynthesis can go on down to the bottom even in winter providing there is a sufficiency of plant nutrients, and the mere closing of the dam might be enough to start off a phytoplankton increase by cutting down interchange with the outside loch and enclosing, in winter, nutrient-rich water. In an attempt to test this, the dam was left open from 2 to 11 March. It was closed that day and samples were taken then and 3 days later. The hydrographic data show, however, that there had been very little interchange with outside owing to poor tides and there was also no significant change in the phytoplankton in the 3 days although it had decreased greatly from the maximum on 2 March. The experiment therefore failed in its object.

On 22 March a fertilization was made using 42 lb. superphosphate and 67 lb. ammonium nitrate. The added phosphate had, as after the previous fertilization, disappeared before samples were taken the following day. Ammonia and nitrate, however, showed an increase at the surface which lasted for 2 days. Diatom numbers had fallen still further from 14 March and continued to do so in spite of the fertilization, although there were still between 10,000 and 30,000 per ml. present at the surface and 1 m. Dinoflagellates on the other hand showed a distinct increase at the surface. The form causing it was a *Gymnodinium* sp. and *Oxyrrhis marina* was numerous on the 26th at 2 and 3 m.

That appreciable photosynthesis had taken place was shown by the abrupt rise in pH at the surface and 1 m. immediately following fertilization. The attached algae were noted as just beginning to grow and, since the rapid rise in pH and the disappearance of the nutrients are much more than could be accounted for by the comparatively small numbers of diatoms and dinoflagellates present, it is probable that the attached algae were responsible. This is confirmed also by the transparency measurements which show only a slight decrease when compared with previous fertilizations.

On 2 April a fertilization was made using 12·4 lb. mono-ammonium phosphate and 103 lb. of ammonium sulphate. Neither the phosphate nor the ammonia showed any appreciable increase when the loch was sampled the following day. Hydrographic conditions were not very stable but there was a marked rise in pH. Diatom numbers had fallen still further since the last fertilization and remained steady at about 10,000 cells/ml. *Chaetoceros simplex* still predominated although *Thalassiosira nana* was also numerous. Dinoflagellates had increased at the surface and decreased at 1 m. since the last visit but fertilization resulted in a marked rise at both depths, up to nearly 5000 and 3400 cells/ml. at 0 and 1 m. respectively. *Gymnodinium* spp. were again mainly responsible. On this occasion the Pulfrich absorptiometer was not available and the transparency was measured by the Secchi disk only; it showed a slight decrease. In the earlier fertilizations there was a good agreement between the phytoplankton and the Secchi disk readings (Fig. 4).

By now, April, the attached algae were obviously competing successfully with the phytoplankton for nutrients and the testing of the remaining nitrogen salts (ammonium chloride and urea) was deferred till the following winter. The algae remained rich during the summer of 1945 and were still abundant in the autumn so that it was not till January 1946 that it was considered safe to do further fertilizations.

The loch was then in a condition very different from what it had been in 1945. Phytoplankton was very scarce with numbers of only 10 or 20 cells/ml. as against the thousands of the previous year. In addition plant nutrients, though not abundant, were present in sufficient quantity to allow plant growth. As in 1944–45, the dam had been opened during the autumn months and was closed at the end of December so that the great difference in the quantity of plankton in the 2 years cannot be explained thus.

A fertilization was made on 10 January with 42 lb. superphosphate and 112 lb. ammonium chloride and another on 23 January with 42 lb. superphosphate and 56 lb. urea. At neither time was there any increase in the phytoplankton, nor was there any important increase in the amounts of nutrients in the water although there was a short-lived rise in soluble phosphorus at the surface after the second fertilization.

At the time of the first fertilization the loch level was unusually high and it fell rapidly during the following days; it was estimated that the loss during the period of this fertilization amounted to about a third of the total volume of Loch Craiglin. Some of the fertilizer must undoubtedly have been lost in this way and it may partly account for the lack of any increase in nutrients. During the second fertilization there was no appreciable change in loch level.

The reason for the failure of these two fertilizations to produce a phytoplankton increase is not known, but several suggestions can be made. Compared with 1945 there was an insignificant number of diatoms present initially and although the shore algae appeared to be negligible, the proportion of diatoms to attached algae may still have been too small for the diatoms to compete successfully for the nutrients. On the other hand, the fact that nutrients were present before fertilization seems against this explanation. The considerable fall in loch level may have carried away both the nutrients and the phytoplankton.

The weather was unfavourable for diatom growth; during the first experiment the loch was frozen over several times and the light thus cut down; during the second it was overcast, wet and stormy. In view of the success of Miss Stanbury's tests which were made on these fertilizers also, it seems unlikely that they were at fault, though she noted a delay in diatom growth with urea as a source of nitrogen when compared with the others.

It must be admitted, however, that none of these explanations is very convincing and that there may be other factors, of which nothing is known, playing a more important part.

Diurnal variation. In shore pools there is normally a considerable diurnal fluctuation in hydrographic conditions and it was thought that this might be true in Loch Craiglin also. In conjunction with an experiment on the vertical migration of *Euglena* (see below), samples of the water were taken at a series of depths every 4 hr. over 24 hr. in August. The weather was calm and bright. During the period of the experiment a high tide in Sailean More caused an influx of open loch water which would affect the results. There was an appreciable diurnal temperature range at the surface which was still noticeable at 1 m. The changes in pH value and percentage oxygen saturation are, however, not related to light and dark at Station I as was expected. Samples taken close inshore where *Ruppia* was growing luxuriantly did show a rise in pH during the day up to nearly 10. A point of interest was the peak in oxygen saturation at 4 p.m. at 2 m. which may be related to the abundance of *Euglena* at that depth.

Occurrence of Euglena. Occasionally in Loch Craiglin very large numbers of a species of *Euglena* (kindly identified by Prof. F. E. Fritsch as *E. proxima*) were present. These were comparatively large (about 70μ long) and might be present in such numbers that the water samples were bright green. Although holotrophic they never appeared in numbers at the surface and were usually most common at or near the boundary between oxygenated and oxygen-free water. They were often found richest in samples smelling of hydrogen sulphide but the numbers fluctuated widely from one depth to another and from day to day so that they apparently occupied a rather narrow zone. They occurred both in winter and in summer although the highest numbers (40,000–54,000 per ml.) were in summer.

Because of this peculiar depth distribution it was thought that their light requirements might be low and that they might migrate towards the surface at dusk and dawn. A series of pump samples was therefore taken at four depths at 4-hr. intervals, from 8 a.m. on 4 August to 4 a.m. on 5 August 1944.

To ensure that the whole water column was sampled fairly evenly, the mouth of the hose in taking each sample was rapidly raised and lowered between

0 and 1, 1 and 2, 2 and 3 or 3 and 4 m. until an adequate amount (about 7 l.) had been taken from each depth. This was well shaken and a subsample drawn off and preserved. The results (Fig. 10 and Table I) were unexpected and are not easy to explain. At no time did the *Euglena* appear in numbers in the water above 2 m. They were always most numerous between 2 and 3 m. except at 4 a.m. when there were slightly more between 3 and 4 m. than between 2 and 3 m. During the course of the experiment there was a slight increase in total numbers at 12 noon but a steady decrease thereafter so that at 4 a.m. there were only a little more than a third of the maximum number.

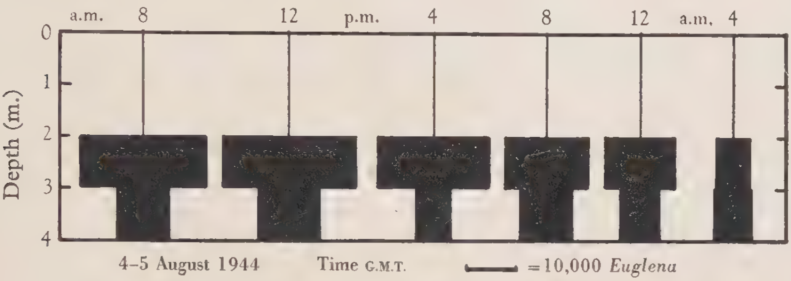

Fig. 10. Vertical distribution of *Euglena proxima* over a 24-hr. period 4–5 August 1944.

TABLE I. DIURNAL VARIATION IN NUMBERS OF *EUGLENA* (NO./ML.)

Depth in m.	Time 8 a.m.	12 noon	4 p.m.	8 p.m.	12 midnight	4 a.m.
0–1	25	Lost	10	25	50	25
1–2	5	5	0	5	15	15
2–3	24,500	26,000	21,500	16,000	13,000	6,250
3–4	10,500	12,000	7,000	10,000	7,500	7,500

The Euglenids obviously do not carry out any appreciable diurnal vertical migration but it is difficult to understand the variation in numbers. They may occur in swarms and a small difference in position may make a large difference in numbers.

Since in spite of their green colour they live so deep in the water, an opportunity was taken when they were numerous of measuring their respiration and photosynthesis. On 23 July 1944 a large sample of water from 3 m. containing 22,400 *Euglena*/ml. was thoroughly stirred to oxygenate it and the changes in oxygen content both in light and dark measured over a period of 4 hr. in the afternoon (12.15–4.15 p.m. G.M.T.) at a depth of 1 m. Samples for the initial oxygen content were drawn off and the samples for light and dark exposure put in bottles, the latter enclosed in opaque black cloth. The bottles in the light showed an oxygen rise of about 0·31 ml. O_2/l. whereas those in the dark showed a consumption of 1·83 ml. O_2/l. This is equivalent to a total oxygen production of 0·024 ml. oxygen per hour per million *Euglena*. It is obvious that although this *Euglena* does carry on photosynthesis, the oxygen thus produced even at a depth of 1 m. is much exceeded by that used up in respiration. Over the whole day, at the depth where they normally occur, photosynthesis must play only a very small part in their metabolism. This was confirmed by an experiment done the previous day when samples of water from each depth (0, 1, 2 and 3 m.) were shaken well to oxygenate them and the oxygen utilization in the dark measured after 24 hr. The utilization was small at the surface (0·14 ml./l.), slightly greater at 1 and 2 m. (0·18 and 0·38 ml./l.) and rose suddenly to 1·74 ml./l. in the 3 m. sample which was slightly green with *Euglena*. The *Euglena* undoubtedly are at times partly responsible for the oxygen lack in the deeper water of Loch Craiglin.

Concentrations of *Euglena limosa* have been described on the surface of tidal mud in the estuary of the Avon (Bracher, 1919) and, since this mud is rich in organic matter and smells strongly of hydrogen sulphide when disturbed it might be expected that the *Euglena* would behave similarly to those in Loch Craiglin. Their reactions are, however, very different. *Euglena limosa* is very responsive to light and when tidal conditions are suitable comes up to lie on the surface during the brightest hours of the day. It is able to survive lack of oxygen for 3 days but not for a week.

Summary and Conclusions

Loch Craiglin cannot be considered as merely an isolated basin of Loch Sween. Its shallowness, the great growth of vegetation round the shore and the fluctuations in salinity make it atypical. On the more complete isolation of the loch with the making of the dam, these conditions led to a lack of circulation, a consequent development of hydrogen sulphide in the deep water and very high pH values near the surface. One could not therefore expect the plankton to be very similar to that in the outside loch (see, however, Marshall, 1947). Unfortunately there are no records of seasonal variation before fertilization was begun. In spite of these drawbacks Loch Craiglin was a convenient and manageable area for small-scale experiments on fertilization.

The experiments may be divided into two groups, those which were not followed up in detail and those in which the plankton and hydrographic results were followed from day to day. The former, made during the earlier stages of the work, are mainly described in the previous papers and led to the conclusion that the richness in phytoplankton of Loch Craiglin in 1943 was probably caused to a large extent by fertilization. Those of the second group, described above, were made to test special points and different fertilizers. Two experiments made during the summer of 1944 had apparently no effect on the phytoplankton but a third in which a very large excess of fertilizer (ten times the normal quantity) was added, gave a good increase after an initial lag. At that time the attached algae were abundant and their needs apparently had to be satisfied before any nutrients could be used by the phytoplankton.

The remaining experiments, which were therefore made during the winter, showed that commercial ammonium sulphate, ammonium nitrate and mono-ammonium phosphate could replace the sodium nitrate and superphosphate used hitherto. Two further experiments in the following spring using ammonium chloride and urea did not, however, prove effective. All the salts used had been found in laboratory tests by Miss F. A. Stanbury to be suitable for diatom growth, and the reason for the failure of these two in the loch is unknown.

The utilization of the nutrients was extremely rapid even in winter but it is probable that their disappearance is not entirely caused by the phytoplankton or bottom-living algae but partly by adsorption on the bottom mud or by suspended matter. On one occasion it may have been caused by a serious fall in loch level.

The zooplankton which during the first year of fertilizations was richer in Loch Craiglin than in the outside loch diminished in the second year and remained poor thereafter in spite of, or perhaps because of, the intensive fertilizations. The dense phytoplankton and other vegetation raised the pH at times to levels dangerous to animal life.

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STRUCTURE, TADPOLE AND BUD FORMATION IN THE ASCIDIAN *ARCHIDISTOMA*

By N. J. Berrill

From the Plymouth Laboratory and McGill University, Montreal

(Text-figs. 1–6)

Archidistoma is a genus created for a species discovered and described briefly by Garstang in 1891 as *A. aggregatum*. It has been found at different times only in the Plymouth region, the original locality, attached to rock surfaces in a few feet of water. Recently, however, it has been found near Cape Hatteras on the eastern American coast (Van Name, 1945), suggesting either harbour to harbour transportation by ship bottom, or that its inconspicuous appearance has obscured a wide distribution.

This form is of considerable interest as it represents a type less specialized in zooid structure, nature of tadpole, and method of budding than any merosomatous ascidian except the diazonids. Diazonids are oviparous and have the simpler development and tadpole associated with small eggs, although there is a more elaborate branchial sac correlated with the relatively large size of the mature zooid.

COLONY

The colony consists of a brownish tough matrix forming a thin encrustation on stones and shells, with individual zooids (a few millimetres long), partly embedded in the test but for the most part extending freely in clumps usually of three or four. Sand grains and round particles adhere to or become buried within the test, making this form the most inconspicuous of ascidians.

STRUCTURE OF ZOOID

The zooid is divisible into a thorax and a long slender abdomen (Fig. 1). There is no postabdomen, nor is there hypertrophy of the ventral test vessels, thereby segregating *Archidistoma* as a type from that of the synoicids (polyclinids) and the clavelinids respectively. The relatively great length of the oesophageal region of the abdomen also marks it off from the didemnids and *Distaplia*.

Both branchial and atrial siphons are well developed and are independent, the atrial siphon having six unmodified lobes like those of the branchial siphon. This is correlated with the absence of true zooid systems and is undoubtedly a primitive feature.

The thorax is short and wide, as is the contained endostyle. Tentacles are simple and about thirty in number. There are three rows of straight stigmata,

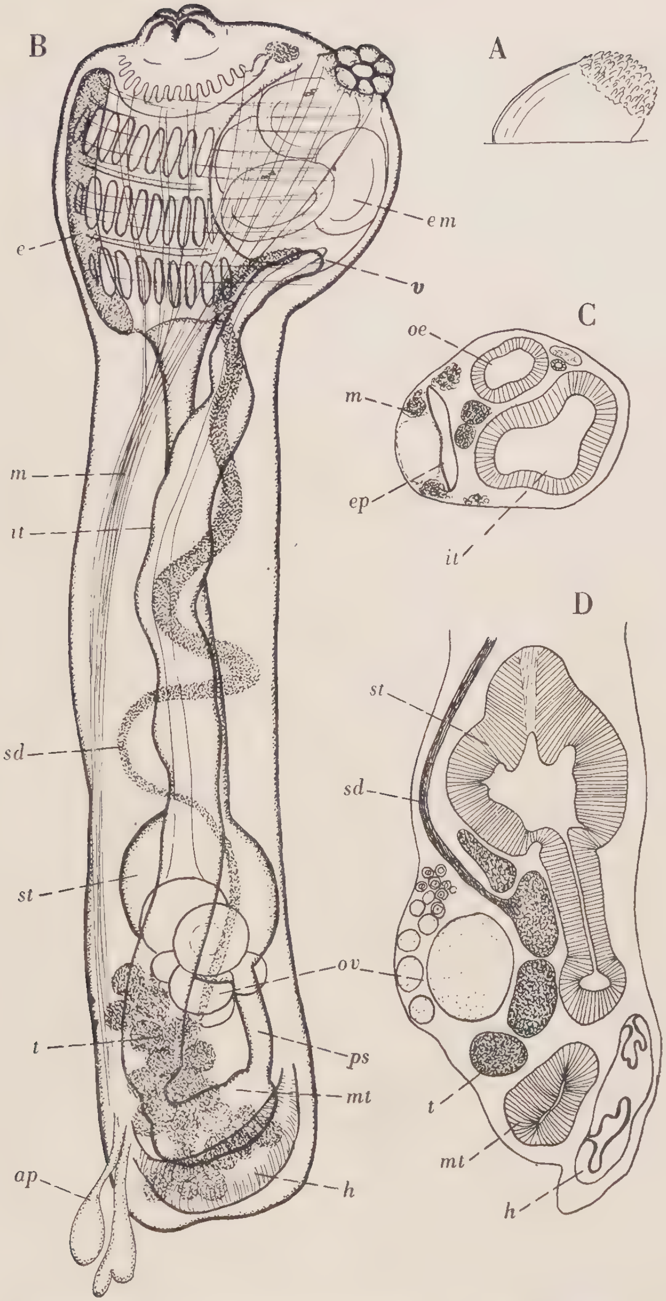

Fig. 1. General structure of *Archidistoma aggregatum*. A, colony growing on bivalve shell, about natural size; B, mature zooid from left side showing organization of thorax and abdomen; C, cross-section through upper part of abdomen showing epicardium; D, longitudinal section of lower part of abdomen showing relationship of gonads and heart to digestive tube. *ap*, ampulla; *e*, endostyle; *em*, embryos in atrial cavity; *ep*, epicardium; *h*, heart; *it*, intestine; *m*, retractor muscle; *mt*, mid-intestine; *oe*, oesophagus; *ov*, ovary; *ps*, post-stomach; *sd*, sperm duct; *st*, stomach; *t*, testicular follicle; *v*, distal ends of oviduct, sperm duct and rectum opening together into base of atrial chamber.

with about ten stigmata per row. A dorsal languet extends into the branchial cavity from each of the two transverse vessels separating the stigmata rows. The rectum, oviduct and sperm duct all terminate well short of the atrial siphon, approximately level with the basal row of stigmata (Fig. 1B).

The abdomen is essentially a long posterior extension of the epidermal body wall and enclosed parenchyma, containing the U-shaped digestive canal, epicardium, heart, gonads, and retractor muscles. The ventral ampullary test vessels project near the ventral end of the heart close to the posterior extremity of the abdomen, and are extremely short.

The retractor muscles are the longitudinal muscles spread somewhat fanwise in the mantle wall of the thorax, converging toward the base and passing down the ventral side of the abdomen as muscle bundles separated partly by the epicardium and partly by the large blood vessel passing from the heart to the endostyle. The muscle fibres terminate at the extreme abdominal tip in association with slight local thickenings of the epidermis.

The digestive canal presents the differentiation characteristic of most small ascidians, whether permanently small or the young of larger forms. A narrow straight oesophagus, with a thin wall of cubical epithelium, descends to the lower part of the abdomen. It enters a globular thick-walled stomach composed of columnar glandular epithelium. The stomach extends as a narrow post-stomach to the base of the abdomen, where it joins the almost horizontal mid-intestine. The latter communicates by another narrow constriction with the lower end of the rectum. The columnar epithelium of the stomach is equally characteristic of the post-stomach and mid-intestine. The rectum, which forms the whole of the ascending limb of the intestine, has a thinner wall consisting of cubical epithelium like that of the oesophagus. The various divisions of digestive canal as a whole appear to be closely related to the locations within the abdominal tube, and it is probable that this is the primitive arrangement, similar digestive canals found in very different locations having become secondarily shifted.

The heart lies horizontally at the base of the abdomen, just below the mid-intestine. The dorsal end opens into vessels branching over the region of the stomach and connecting above with the parenchymal blood channels in general. The ventral end opens into a wide vessel lying between two bundles of muscle fibres and bounded internally by the epicardium. This vessel passes up the whole length of the abdomen and becomes the subendostylar vessel in the thorax.

The epicardium is typical of the great majority of merosomatous ascidians. In the lower third of the abdomen it consists of a single cavity lined by an extremely thin epithelium, lying between the digestive canal and the ventral aortic blood vessel. It ends blindly posteriorly, but anteriorly above the level of the stomach, the right and left divisions, detectable even when fused, become separate from one another and extend as a pair of sacs to the base of the thorax.

There they end blindly as a pair of horns immediately beneath the floor of the pharynx (from which they were originally derived).

The gonads also occupy the position characteristic of most enterogonid ascidians, namely, in the general vicinity of the intestinal loop between the stomach and the mid-intestine. The small spherical testicular follicles extend farther posteriorly to the level of the heart, that is, as far as they can go, and do not extend quite as far anteriorly as the ovary which reaches the lower part of the stomach. To a significant extent, the ovary, or at least the relatively large ova, are surrounded by the follicles of the testis. The oviduct follows the rectum to open alongside the anus into the base of the atrial cavity. The sperm duct does the same except that it takes a somewhat more tortuous course. The arrangement both of the gonads and their ducts is undoubtedly primitive and common to the majority of ascidians.

SEXUAL REPRODUCTION

Eggs pass up the oviduct and undergo their development as far as the active tadpole stage within the atrial cavity, taking up so much space there that the branchial sac may become pushed very much to one side. Fertilization probably occurs within the oviduct, although this is not known for certain. Eggs are of 0·23 mm. diameter and are extremely yolky, closely resembling those of the synoicids and likewise undergoing epibolic gastrulation.

Considerable increase in size occurs during the development of the embryo, although at the time of liberation of the tadpole a mass of relatively large yolky endodermal cells still remain more or less unutilized, lying between the pharynx and digestive canal, alongside the epicardium. The paired peribranchial ectodermal invaginations fuse to form the single median atrial siphon while yet in the embryonic phase.

The tadpole larvae (Fig. 2) have a short free-swimming period, on an average of about 2 hr. Their organization is interesting in several ways, being a generalized type compared with those of the synoicids, didemnids, clavelinids and holozoans.

The larval structures are rather large relative to the size of the trunk. The tail is long, the sensory vesicle large, and the permanent organs occupy practically all the remaining space, as though there had been a restriction of the surface area of the epidermis. The sense organs are typical, though individually relatively large, and consist of a unicellular otolith and an ocellus bearing three unicellular lenses (Fig. 3B). The tail, as in all viviparous (large-egged) enterogonid ascidians, has undergone a 90° torsion, so that the tail fin is horizontal and the nerve, no longer dorsal, runs along one side (Fig. 3C). It has the universal number of approximately forty notochord cells, while the muscle cells, in a relatively advanced state of differentiation, are arranged in series as three bands down each side of the notochord. Anteriorly the three adhesive organs project on long slender stalks, in triangular arrangement, each organ consisting of a central adhesive papilla and a marginal epidermal cup or sucker.

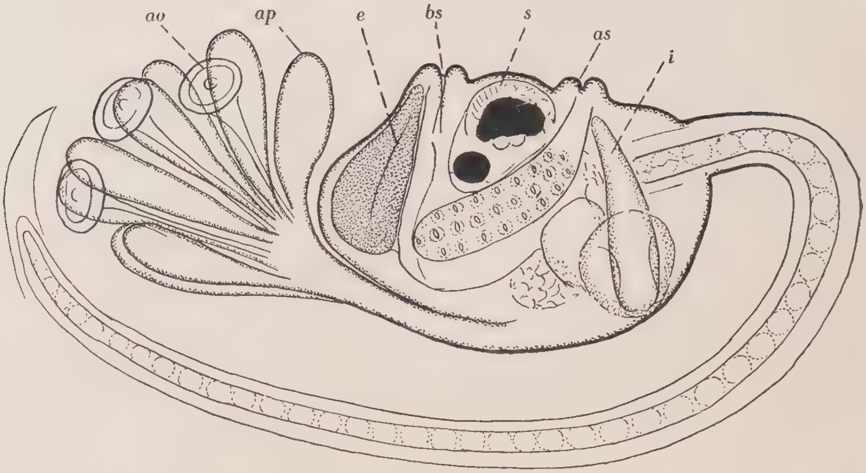

Fig. 2. *Archidistoma aggregatum.* Tadpole larva, with eight ampullae and three adhesive organs anteriorly, a relatively large sensory vesicle, and three rows of perforated stigmata on each side. *ao*, adhesive organ; *ap*, ampulla; *as*, atrial siphon; *bs*, branchial siphon; *e*, endostyle; *i*, intestine; *s*, sensory vesicle.

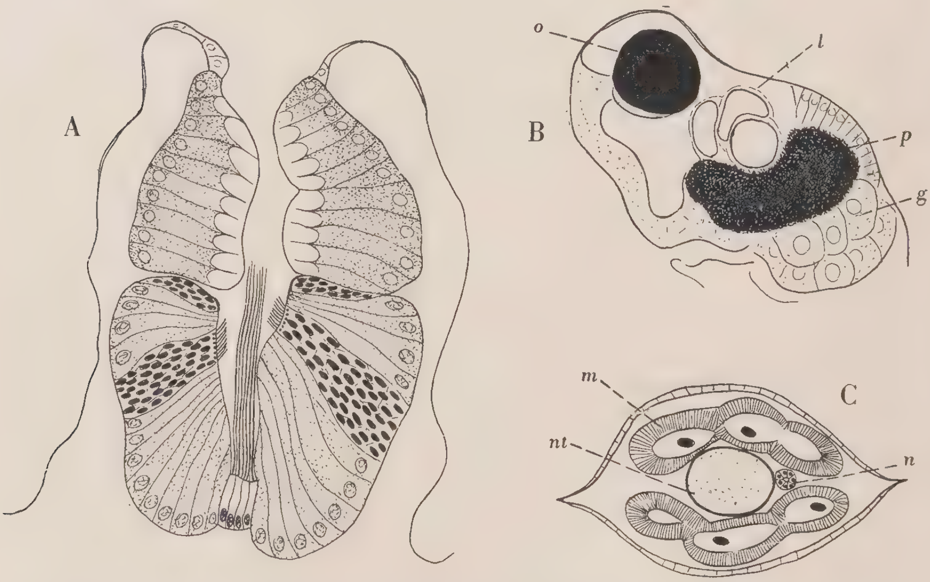

Fig. 3. *Archidistoma aggregatum.* A, section through endostyle of adult, showing lateral bands of large glandular cells alternating with bands of small ciliated cells, and a median ventral band with very long flagella; B, sensory vesicle of tadpole with unicellular otolith, and typical three-lens ocellus; C, section through tail, showing notochord, neural tube, and lateral muscle bands of three cell-rows (highly differentiated). *g*, ganglion cells; *l*, lens cells; *m*, muscle cell; *n*, nerve tube; *nt*, notochord; *o*, otolith; *p*, pigment obscuring retinal cells.

The larval endostyle is relatively large and lies vertical to the main axis. The digestive tube is fairly well differentiated, while the peribranchial sacs, already fused mid-dorsally to form the atrial siphon, are united with the pharyngeal wall on each side and bear each three rows of perforate, definitive stigmata. There are eight or nine stigmata in each row, approximately the same as in fully grown zooids.

From the mid-ventral surface of the trunk of the tadpole, corresponding to the future posterior end of the individual zooid, a slender epidermal process grows out and forwards. From the anterior end of this there extends not only the three adhesive organs described above, but eight club-shaped ampullae, arranged in a ring around the more centrally placed adhesive organs.

After metamorphosis the ventral process expands and grows as the stalk of attachment into which extend the digestive canal, epicardium and heart. The anterior ampullae form an irregular organ of attachment, the adhesive organs having a transient function only.

BUDDING

During the winter, and to a very slight extent in summer months, growth of the colony occurs by budding. The method of bud formation (Figs. 4–6) is simple in the extreme, is found in other ascidians only in the diazonids, and is strikingly reminiscent of *Phoronis*.

The thorax slowly resorbs, a common phenomenon among ascidians. Associated with this, large cells or trophocytes, heavily laden with acquired food reserves, migrate posteriorly and congest the abdomen. They are similar to those that reach and congest the postabdomen of synoicids and the stolonic ampullae of the clavelinids, but here they are confined to the abdomen owing to the absence of any postabdominal extension and the lack of hypertrophy of the test vessels respectively.

Local growth activity of the epidermis then constricts the long abdomen into several oval masses, one constriction usually occurring below the stomach and two above. Only the epidermis plays an active part in the process, the inner tissues (epicardium, both limbs of the digestive canal, etc.) being passive and cut through by the invaginating outer layer.

The process of constriction is a local annular growth of epidermis inwards, the cells of the invading ring not only proliferating but exhibiting a change from cubical to columnar form. The inner end of each cell becomes greatly extended by a large vacuole. A similar vacuolated condition is typical of epicardial cells, at least in fragmenting abdomens. In both the vacuolar region is away from the exposed epithelial surface.

Regeneration occurs subsequently. In this process it is the epidermis that has the relatively minor role, producing only the epidermis of the new outgrowths. The internal structures, both anterior and posterior, are developed from the proliferating ends of that section of the epicardium contained in the isolated piece. The new branchial sac and gut loop thus formed are fitted on to

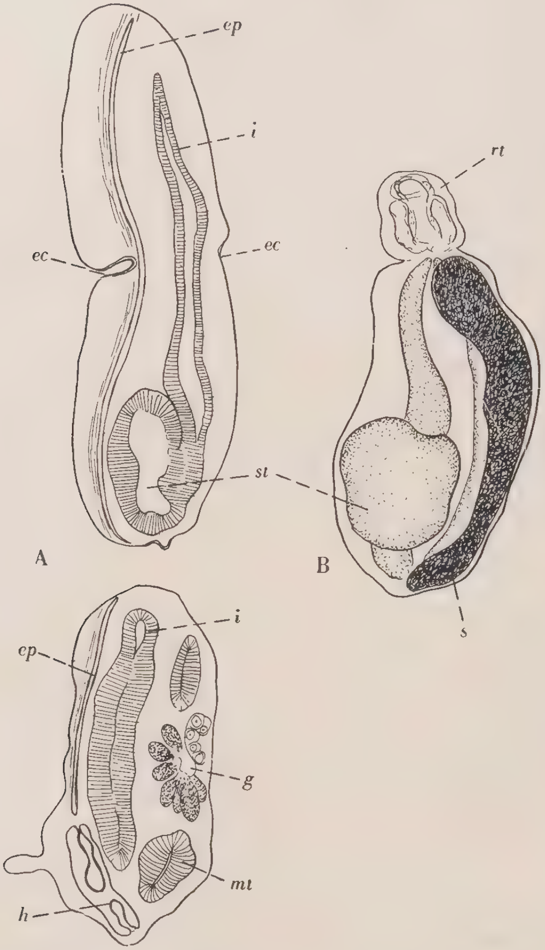

Fig. 4. *Archidistoma aggregatum*. Strobilation and regeneration. A, longitudinal section through strobilating abdomen, showing complete transverse division immediately below stomach, and incomplete constriction in middle part of anterior fragment (thorax resorbed); B, fragment containing original stomach etc., and part of distended sperm duct, regenerating new thorax from upper end of epicardium. *ec*, epidermal constriction; *ep*, epicardium; *g*, gonad; *h*, heart; *i*, intestine; *mt*, mid-intestine; *rt*, regenerating thorax; *s*, original sperm duct; *st*, stomach.

the surviving part of the original digestive canal. The food-laden cells produced during the resorption process become progressively smaller and more numerous, yielding their reserves in nourishing the growing tissues.

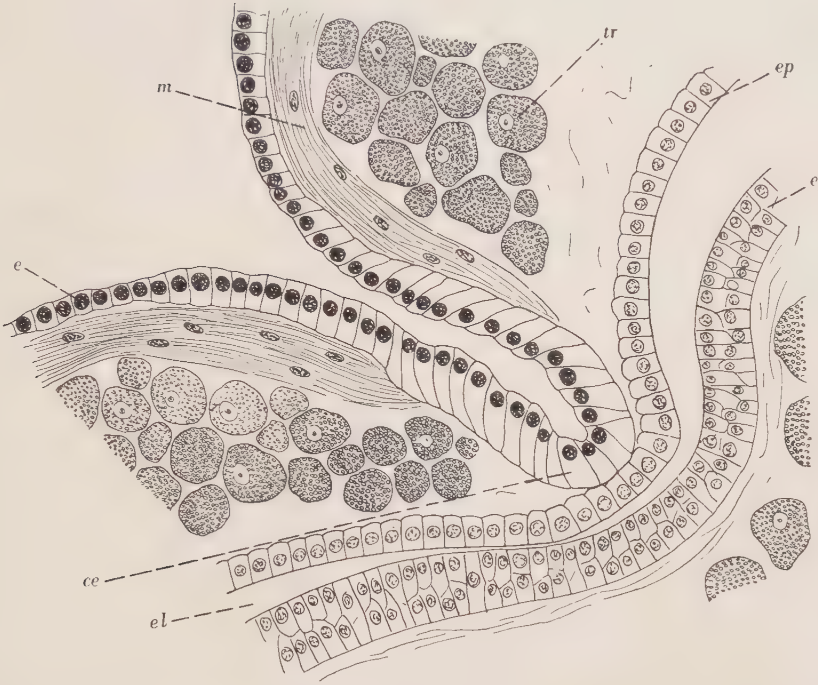

Fig. 5. *Archidistoma aggregatum*. Higher magnification of epidermal constriction shown in Fig. 4, showing epidermis cutting in through muscle and trophocyte layers and impinging on epicardium. *ce*, enlarged epidermal cells of constricting region; *e*, normal epidermis; *el*, lumen of epicardium; *ep*, lining cells of epicardium; *m*, retractor muscle; *tr*, trophocyte.

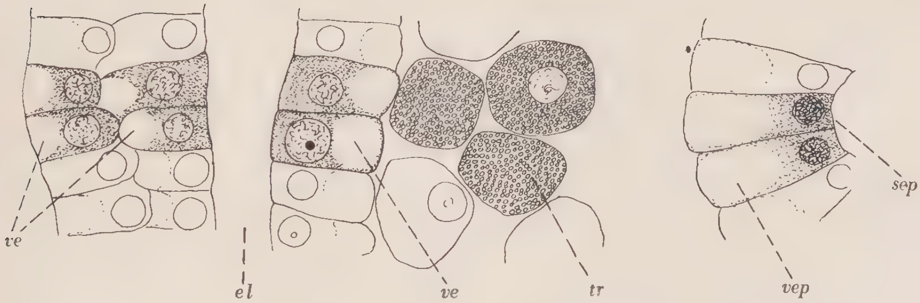

Fig. 6. Enlarged view of constricting epidermal cells and activated epicardial cells (× 1000), both showing vacuolization of the cells on the side away from the outer surface of the body and the epicardial cavity respectively. *el*, epicardial lumen; *sep*, outer surface of epidermis; *tr*, trophocyte; *ve*, vacuole of epicardial cell; *vep*, vacuole of epidermal cell in constricting region.

In so far as the general structure of the zooid appears to be comparatively primitive, and the manner of bud formation undoubtedly as simple as it can be, the type of budding in *Archidistoma* may reasonably be regarded as the most primitive found in the ascidians.

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THE DEVELOPMENT, MORPHOLOGY AND BUDDING OF THE ASCIDIAN *DIAZONA*

By N. J. Berrill

From the Plymouth Laboratory and McGill University, Montreal

(Text-figs. 1–7)

Diazona is represented in European waters only by *Diazona violacea* Savigny. It is a compound ascidian forming massive colonies of spectacular size and appearance. In many ways it is the most interesting of all ascidians, for in its adult structure it straddles two commonly accepted orders and in itself is a strong argument against such a division; it is the only oviparous and small-egged compound ascidian, two features undoubtedly primitive; and its manner of budding is the simplest and probably is the basic type for the group as a whole. Only fragmentary descriptions of the morphology and reproduction exist, and a more or less complete account of the various stages of the life cycle may be of some value. The family Diazonidae includes, in addition to *Diazona* itself, the genera *Tylobranchion* of subantarctic regions, and *Rhopalea* of Mediterranean and northern waters. In its entirety *Diazona* appears to link with such divergent forms as *Ciona* on the one hand and *Archidistoma* on the other. The fact that *Diazona* is obtained by dredging in relatively swift offshore waters and lives poorly in an aquarium probably accounts for the existing unsatisfactory state of knowledge of most of its phases. Most of what is known concerns asexual reproduction; and attention has been given, at various times, primarily to the process of regeneration, rather than bud formation, for example by Della Valle (1884), Caullery (1914), Oka (1906) under the name *Aphanobranchion*, and by Salfi (1926).

The material of the present account was collected at various times in the Plymouth area from the Mewstone and Eddystone grounds.

GENERAL STRUCTURE

Diazona is usually found as large massive colonies exceeding in bulk all other known compound ascidians, both in aggregate and individual. All but the anterior ends of the zooids are embedded in a massive firm gelatinous matrix of tunicin. The individual zooid represents a combination of characters that is unique (Fig. 1). It is merosomatous, that is, the body is divided into thorax and abdomen, the abdomen lying posterior to the thorax and joined to it by a relatively narrow oesophageal region. A slender vascular process descends from the posterior part of the abdomen far into the common test, branching and bearing a number of blind ampullary sacs. The vessels remain narrow, never becoming enlarged as in *Clavelina* (they contain an afferent and efferent vascular current). There are independent branchial and atrial siphons, and there is no tendency for individuals to become arranged in systems.

The thorax is relatively large, though seldom expanded in specimens in aquaria, and has sixty to seventy rows of stigmata in each branchial wall. Vascular papillae grow into the branchial cavity from the inner wall and bear the inner longitudinal vessels. Secondary papillae are absent, and the branchial sac is not otherwise complicated. Longitudinal muscles extend the length of the thorax and converge in the oesophageal region into a narrow band on the ventral side. Posteriorly in the abdomen the band is divided ventrally by the pericardium, and the two bundles become separately inserted at the base of the abdomen. White reflecting pigment cells congest the endostyle, peripharyngeal bands, and the dorsal lamina, making the combined system very

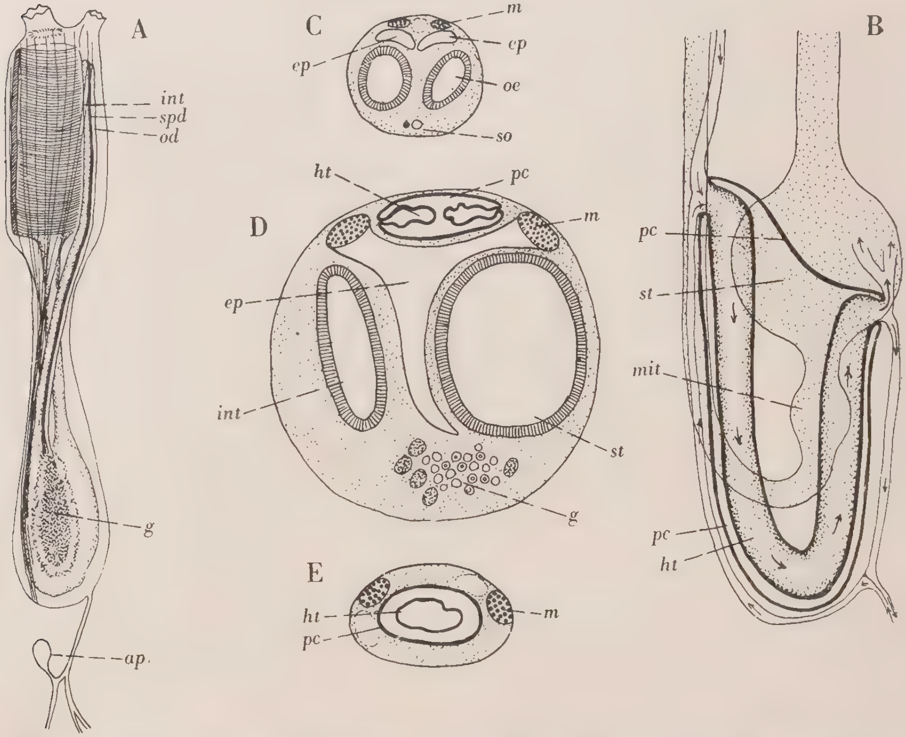

Fig. 1. Morphology of *Diazona violacea*. A, complete mature zooid; B, heart, pericardium and digestive canal, reconstructed from serial sections; C, cross-section through oesophageal region, showing paired epicardial sacs; D, section at level of stomach, showing fused epicardia and heart; E, section posterior to digestive canal and epicardium, showing heart and terminal region of heart. *ap*, ampulla of stolonic vessel; *ep*, epicardium; *g*, gonad; *ht*, heart; *int*, intestine; *m*, muscle; *mit*, mid-intestine; *od*, oviduct; *oe*, oesophagus; *pc*, pericardium; *so*, sperm duct and oviduct; *spd*, sperm duct; *st*, stomach.

conspicuous. The dorsal lamina is basically composed of a languet projecting into the branchial cavity corresponding to each of the sixty to seventy transverse blood vessels separating adjacent rows of stigmata.

The abdomen contains, in addition to the longitudinal muscles, the loop of the digestive canal, heart, epicardium, and the reproductive organs. The form of the digestive canal is obscure in whole specimens but is readily seen in regenerating forms and from serial sections. The long narrow oesophagus expands into a globular stomach. Posteriorly the stomach constricts and then the canal expands again to form the mid-intestine, which opens into the base of the loop, the intestine proper or rectum. This last ascends the abdomen and thorax to open close to the atrial siphon.

The pericardium and heart occupy the lower half of the abdomen on the ventral side. The pericardium is a simple sac, blind at the base, extending higher on the left than the right side, and wider laterally than dorso-ventrally. The heart is a deep invagination of the pericardial wall extending the whole length of the lateral margin, from the high left shoulder of the pericardium to its base and along the right side to the region of the stomach, forming a deep V-shaped tube. In a functional sense the invagination is closed to form a deep tube of contractile cardiac tissue. Morphologically it remains continuous with the pericardium and the cardiac lips merely approximate to form the so-called 'raphe' of the heart. The vessels connected with the two ends of the heart are similar to those of other merosomatous forms and of *Ciona*. Entering the high ventral end are two vessels, one of which extends through the oesophageal region and becomes the sub-endostylar vessel. The other passes posteriorly and enters the narrow stolonic vessel together with a similar vessel from the dorsal end of the heart. The two channels thus formed are separated by a mesenchymatous septum. The dorsal end of the heart is also supplied with vessels from the stomach region and the blood sinuses of the body as a whole, of blastocoelic character.

The epicardia for the most part are fused to form a median chamber, as in all other merosomatous ascidians except *Euherdmania* and the Didemnidae. They end blindly just beneath the posterior wall of the branchial sac, one on each side, and extend as separate tubes through the oesophageal region, lying between the digestive canal and muscle band. Near the stomach fusion occurs to form a single large cavity apposed ventrally to the pericardium, with a lateral horn reaching the muscle band on each side, and a median dorsal extension between the descending and ascending limbs of the digestive canal. Posteriorly it ends blindly at a level intermediate between the end of the pericardium and the bend of the gut.

The gonad is a large hermaphrodite gland consisting of a centrally situated ovary with numerous and relatively small eggs, with numerous peripheral testicular follicles, the whole mass lying across the loop of the digestive canal posterior to the oesophagus, on the left side. Both sperm duct and oviduct are fairly straight and accompany the rectum to open near the anus just below the atrial siphon. This proximity, together with the small size of the eggs, assures a condition of oviparity.

SEXUAL REPRODUCTION AND DEVELOPMENT

Sexual maturity is reached in July and lasts into September. Eggs are liberated in fair number and develop outside of the colony. They are very similar to those of the Ascidiidae, both in size (0·1 mm.), and in the character and number of the outer and inner follicle cells (Fig. 2A). The outer cells are typical, neither exhibiting the flattening out over the chorion as in viviparous forms, nor specialized as 'floats' to the extent found in *Ciona intestinalis*, *Corella parallelogramma* and *Ascidiella aspersa*.

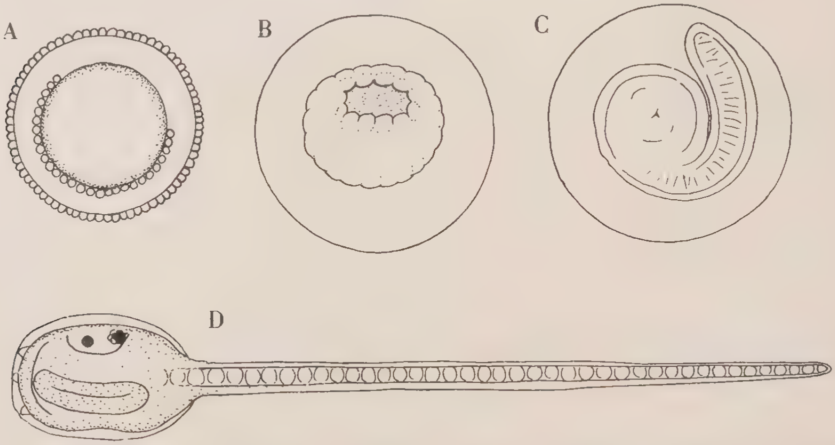

Fig. 2. *Diazona violacea*, development of tadpole. A, egg; B, gastrula; C, embryo; D, tadpole.

At 16° C., gastrulation occurs after about 5 hr., and is enbolic as in most ascidian eggs of this size (Fig. 2B). The transparency of the egg is indicative of a relatively small amount of yolk. The tadpole (Fig. 2D) hatches by digestion of the chorion after 26–27 hr. at the above temperature. Tadpoles at first are positively heliotropic, and the free-swimming period is normally from 20 to 24 hr. In general, the tadpole larva is much like that of the above three forms, both in size and appearance. The endostyle is more or less horizontal at this stage. The sensory vesicle contains the usual single-celled otolith and 3-lens ocellus. The three adhesive papillae are simple. There are about forty notochord cells in the tail, and the cuticular tail fin is virtually absent.

The process of metamorphosis is prolonged (Fig. 3). After fixation by the adhesive papillae, the tail absorbs and the anterior end of the trunk grows out as the preoral lobe, as in *Ciona*. Rotation occurs, and after 10 or 11 days at 16° C., the siphons are contractile and the heart is beating. The characteristic rythmical reversal of heart beat is exhibited from the beginning. The cilia of the gill slits beat actively about 16 days after fixation. During this period the preoral lobe grows as the stalk attaching the young Diazonid individual to the substratum. Finally it is a vertical stalk as long as the trunk proper, divided basally into two or three wide anchoring lobes. As in *Ciona*, *Corella* and *Ascidia*, at this stage, there is a single branchial siphon and in place of a median-dorsal atrial siphon there are a pair of very widely separated peribranchial siphons, extending laterally from the body wall. Each connects with a peribranchial sac associated with two large protostigmata. The digestive canal lies more or less horizontally immediately beneath the branchial sac, as in *Ciona*, and at this stage shows no inclination to descend into the stalk. The heart is simple and lies directly between the base of the endostyle and the bend of the intestine. A group of longitudinal muscles extends from the trunk into the

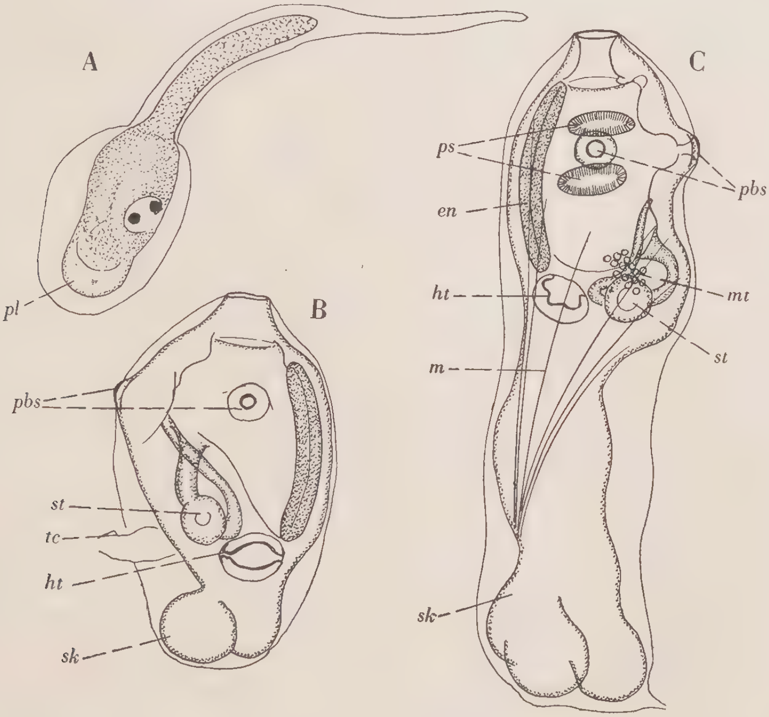

Fig. 3. *Diazona violacea*, post-larval development. A, metamorphosing tadpole with preoral lobe. B, stage 9 days later with active heart and siphons but no cilia; C, stage 5 days later (at 16° C.) fully active, with paired peribranchial siphons. *en*, endostyle; *ht*, heart; *m*, muscle; *mt*, resorbed muscle cells of tail; *pl*, preoral lobe; *pbs*, peribranchial siphons; *ps*, protostigmata; *sk*, stalk; *st*, stomach; *tc*, tunic remnant of tail.

stalk, and when contracting causes the ascidian to bend in an arc about the junction of stalk and trunk. An avoidance reaction is strongly suggested.

This is the latest stage to which the oozooid has been raised, and there is a remarkable resemblance to the equivalent stage of *Ciona*.

ASEXUAL REPRODUCTION

Asexual reproduction or budding concerns entirely the establishment and growth of the colony. It does not increase the number of colonies. The various phases of growth and reproduction are seasonal. A colony undergoes a process of bud formation in the late autumn and early winter. During late winter and early spring the buds regenerate, and in late spring and early summer become fully grown and sexually mature. There is then a sexual breeding season of from 6 to 8 weeks, and the cycle commences once more. Each zooid produces from three to eight buds in healthy colonies. By estimating the number of zooids in colonies, some indication of the age of a colony can be obtained. Maximum-size colonies thus appear to be 4 or 5 years old. There is no reason to suppose that the annual cycle could not be repeated indefinitely, but it is most probable that colonies above a certain size become dislodged from their attachment, partly because of the relatively greater exposure to the action of the strong currents in which they live, and partly because increase in colony size removes individuals farther and farther from the base of attachment, the matrix of which must be kept firm and healthy by the activity of their stolonic vessels. Since these vessels degenerate in winter during the process of budding, the likelihood of a large colony sloughing off must be great.

In the early fall, a few weeks after the cessation of sexual breeding, progressive changes take place in the zooids. The thorax of each shrinks, and no longer projects from the colony surface, the latter becoming finally perfectly smooth and of a soft cartilaginous texture.

The shrinkage of the thorax proceeds (Fig. 4) and is due to the activity of certain cells, for convenience called trophocytes. These cells, of obscure origin, derived probably from blood cells, appear throughout the thorax and grow in size as they accumulate within themselves a pseudovitellus or protein reserve. They probably arise in the same way as, and are homologous with, the cells described by Spek (1927) from living vitally stained tissues of *Clavelina*. A comparable histological study of resorption in *Diazona* along such lines would be of interest. Their appearance or growth occurs simultaneously with a shrinkage or autolysis of the differentiated thoracic structure, and is followed, as in *Clavelina* and many other forms, by a migration of the trophocytes towards the posterior end of the zooid. The cells are too large to enter the narrow stolonic vessels (which in *Clavelina* are large and become congested), and it is the abdomen and oesophageal region that becomes distended with them. The thorax survives for a while as a faint ghost of itself, but finally disappears entirely. The trophocytes form a nutritive reserve, but they neither take an active part in the formation of buds nor contribute to new structures apart from the maintenance of the nutritive medium in which such structures develop. Bud-formation is essentially a process of epidermal strobilation or constriction. As the trophocytes withdraw from the anterior regions, transverse constrictions develop that cut deep into the internal tissues. The narrow oesophageal 'neck' is involved to a varying extent, the abdomen from the posterior end to just anterior to the stomach not at all. The constrictions for the most part occur in the intermediate zone anterior to the stomach. As far as can be determined the constrictions appear and develop simultaneously, finally isolating masses more or less at the same time, with the exception of the most posterior constriction. This last constriction may commence later than the more anterior, but it is also possible that the belated separation of the bud is due to the greater growth of the process. Anyhow, it is a typical condition for four or five more or less spherical masses to be isolated in series immediately anterior to, and in line with, the posterior part of the abdomen, with the proximal bud regenerating from the anterior end and still in process of constriction posteriorly. Finally, this bud too is isolated and the large abdominal remnant regenerates anteriorly. Frequently a mass may undergo isolation in the anterior oesophageal region, the region immediately posterior to it evacuated, and the posterior strobilating part connected with it by 'ghost' tissue. It raises the question of the relative roles of epidermis and internal tissues.

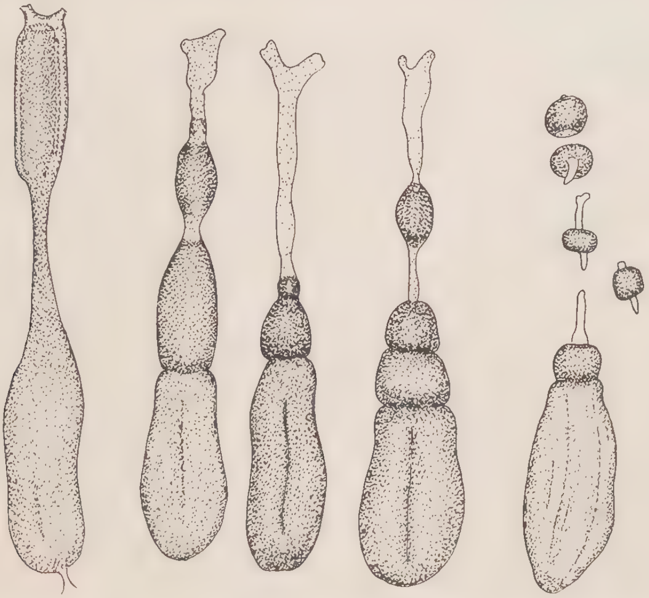

Fig. 4. *Diazona violacea.* Five zooids illustrating stages in resorption, posterior congestion by trophocytes, and strobilation.

Two phenomena require elucidation—the fact of constriction itself, and the virtual spherical shape of the constricted mass. Sectioned material confirms the conclusion derived from direct observation on intact constricting zooids, that there is necessarily a real growth of epidermis in order to produce the deep folds (Figs. 5, 6). In the narrow band of the constriction itself the epidermal cells are unusually large and show every appearance of extensive growth, pressing against, and in effect dividing, the trophocyte mass, actually cutting through the longitudinal muscle, epicardium, and limbs of the digestive canal.

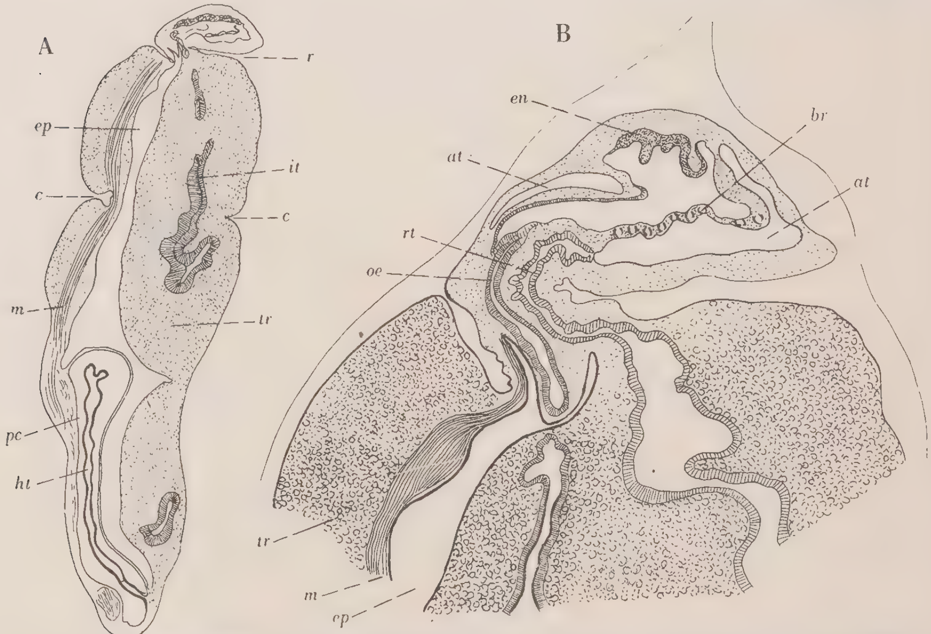

Fig. 5. *Diazona violacea*. Longitudinal sections through strobilating and regenerating abdomen, showing anterior regeneration of thorax from horns of epicardia, a mid-abdominal constriction, and the persistence of the heart and other structures. *at*, atrial cavities; *br*, branchial wall; *c*, constriction; *en*, endostyle; *ep*, epicardium; *ht*, heart; *it*, intestine; *m*, longitudinal muscle; *oe*, new oesophagus; *pc*, pericardium; *r*, rectum; *rt*, new rectum; *tr*, trophocytes.

The epidermal tissue grades gradually from the actively growing tissue at the cutting surface back to the inactive tissue at the original surface of the zooid, indicating a slow recovery of normal cell size and appearance with the cessation of growth. All of the internal tissues are purely passive, playing no part in the process of constriction itself.

When constriction nears completion and later until regenerative processes modify the initial shape, a bud is practically spherical. This appears to be due to a freedom of movement of the large trophocytes, so that the shape of the whole contained mass of them conforms to the action of surface forces, as would a mass of small greased balls within a contracting envelope.

Salfi (1926) discusses the process of bud production in *Diazona* in terms of Child's 'physiological isolation', but whatever this may be it does not seem to apply here. Resorption of the thorax is a common phenomenon among compound ascidians and is generally followed by its regeneration from the oesophageal region or from the abdomen. In *Diazona* this process is combined with that of strobilation of the anterior abdominal and oesophageal region. The posterior abdominal region regenerates anteriorly in the usual way. Strobilation itself is something clearly distinct from 'physiological isolation', a term applied by Child to the production of buds by otherwise intact organisms. One cannot avoid the conclusion that physical forces are at least a part of the controlling agent. Excluding the residual region, constrictions appear so as to segregate masses initially with the long axis approximately the same as the transverse. Since the tapering width of the strobilating region is determined by the original shape together with the degree of trophocyte congestion, the equality of the two axes strongly suggests an effort to produce spheres, as a liquid cylinder breaks up into spherical drops as a result of surface-acting powers. If there is any truth to this, then it implies that the differential growth of the epidermis which is the actual constriction is a local response to physical forces related to surface tension.

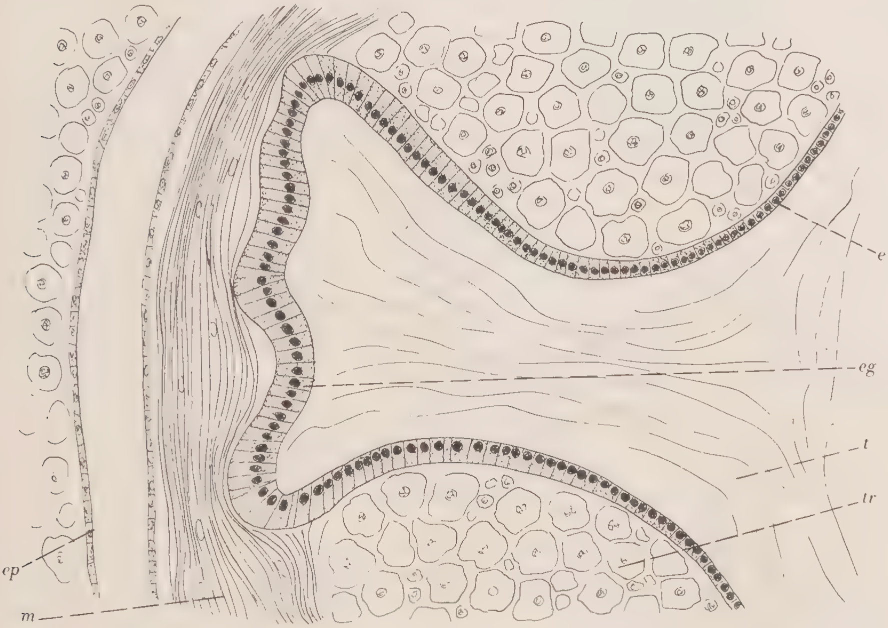

Fig. 6. *Diazona violacea*. Longitudinal section through abdominal constriction, showing active epidermal growth at constriction surface, cutting through passive internal tissues. *e*, normal epidermis; *eg*, growing epidermis forming constriction; *ep*, epicardium; *m*, longitudinal muscles; *t*, tunicin secreted in constriction groove; *tr*, trophocytes.

The phenomena of reconstitution have been studied by Salfi in some detail. His observations are more or less confirmed, namely, that the fragments of the epicardium, longitudinal muscles, and descending and ascending limbs of the digestive canal survive, and that regeneration at the anterior and posterior surfaces is due almost entirely to epidermal growth forming the new epidermis, and the epicardium the internal structures (Fig. 7).

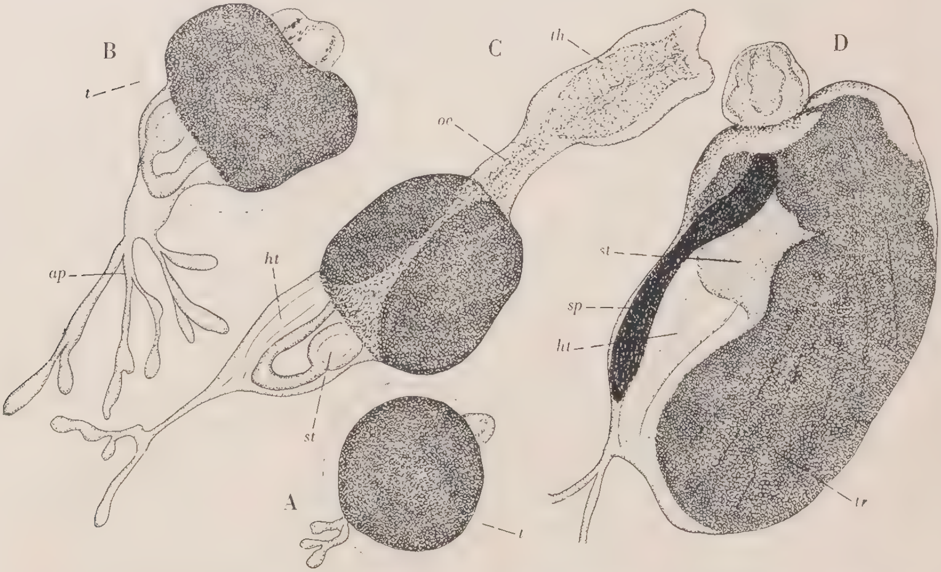

Fig. 7. *Diazona violacea.* Isolated buds in process of regeneration. A, bud still spherical and just starting anterior and posterior regeneration (dotted line indicates zone of new tunic); B,C, later stages of regeneration; D, anterior regeneration from large posterior abdominal fragment containing old heart, stomach, distended sperm duct, etc. *ap*, ampullary stolonic vessels of test; *ht*, heart; *oe*, oesophagus; *st*, stomach; *sp*, sperm duct; *t*, new test substance; *th*, new thorax; *tr*, trophocytes.

The new thorax, including the branchial sac, atrial sacs, ganglion, and thoracic part of the intestine, but excluding the epidermis, arises from tissue formed by the proliferating anterior end of the epicardium. The new intestine becomes joined to the remnant of the old. There is some indication of cellular replacement within the old sections of the digestive tube even though there is continuity in gross appearance. The regenerating branchial sac develops about seventeen rows of stigmata, the number varying somewhat with the size of the bud, but always a number far less than that typical of mature adults. Additional rows are added after the reconstituted zooid becomes functional, during renewed growth. The early stages of thoracic morphogenesis, other than the general epicardial origin, has not been determined. Posteriorly regeneration is a little more complex in origins though not in structures produced.

The epidermis grows out and branches terminally to form clusters of stolonic vessels. As far as can be determined from somewhat limited material, the two posterior ends of the digestive canal fragments unite and the loop grows posteriorly keeping pace with the epidermal outgrowth, and at an early stage shows differentiation into stomach, post-stomach, and mid-intestine regions. The new pericardium and heart appear to develop from the posterior extremity of the epicardium, as in *Aplidium* (Brien, 1925). Unlike the majority of ascidian buds, therefore, reconstitution of the new zooid is fundamentally a typical regeneration process from anterior and posterior surfaces, rather than either reorganization or a virtual complete development.

With continued growth of the structures thus established, the opaque mass of the original bud gradually becomes progressively transparent and eventually forms an elongated oesophageal region of the reconstituted individual. This is complete in early spring, and growth to sexual maturity occupies a succeeding 2 or 3 months.

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THE ECOLOGY OF THE AMPHIPODA OF THE SOUTH OF THE ISLE OF MAN

By N. S. Jones, M.Sc.

Department of Zoology, University of Liverpool

(Text-figs. 1, 2)

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INTRODUCTION

An ecological survey of the Amphipoda on the shores of the Port Erin district was begun in November 1939. After a few months the work was interrupted by the war, but was recommenced early in 1946. In the later period the survey was extended to include the offshore grounds.

The object of the survey was in general to revise the records of the Amphipoda of the area and to obtain an estimate of the relative abundance of the species present, and in particular to provide additional information about the habitat of each species. It was thought that valuable results would be obtained by intensive collecting over a restricted area.

The majority of the records previously published were made by A. O. Walker over 50 years ago, but a few additions have been made since (Moore, 1937). It is interesting to note that of 121 species previously known 114 were collected during 1946–47. The remaining seven have each been recorded on only one occasion and are probably very scarce. An additional thirty-five species are here recorded for the first time (Appendices I and II). Some of these additions are due to recent taxonomic revisions such as that on

Marinogammarus (Sexton & Spooner, 1940), but the majority are the result of more intensive and specialized collecting of the order. The total number of species now known from the area is 156.

The taxonomy of the Amphipoda has been fairly well worked out in British waters. Although certain genera would repay revision there are probably very few species occurring around the British Isles that have not been described, except perhaps in the deep water to the west of Ireland. During the course of this work not one individual was obtained that could not be referred to an existing species.

It is not possible in a survey covering a large number of species to work on strict quantitative lines. On most types of shore exact quantitative methods are difficult to achieve and offshore they can only be attained on suitable ground by the use of the bottom-sampler which is not an ideal instrument for the collection of small Crustacea. However, in the course of a large number of shore collections and dredgings a fair estimate can be made of the relative abundance of the species found. Often the numbers were greater than had been expected.

Information on the habitats of amphipod species is generally limited, except for those of a few genera which have been recently revised and those of intertidal sands and of estuaries. The more important papers published with reference to this aspect are those of Reibisch (1905–6), Crawford (1937*a*, *b*, *c*), Elmhirst (1931), Southern (1915) and Watkin (1941). Lists of species from various habitats are given by Chevreux & Fage (1925) and Stephensen (1929). Pirlot (1932*a*, *b*, *c*) discusses the influence of a burrowing mode of life and a tendency towards parasitism upon the mouthparts of Amphipoda.

THE AREA UNDER INVESTIGATION

The area within which this survey was made included the coastline within a radius of 10 miles from Port Erin. Some stations were worked more intensively than others, but collections were made at sufficient localities to be representative of the whole shore. The offshore work was mainly carried out in depths of less than 40 m. within a few miles of Port Erin Bay. Some hauls were taken in depths down to 84 m. at distances up to 10 miles from Port Erin, but the deeper water cannot be considered thoroughly investigated.

A description of the shores near Port Erin with charts is included in Moore (1937) and the closer offshore grounds are dealt with by Jones (1940). It may be added that the sea bottom slopes gradually to a depth of about 45 m. at a distance of roughly 6 miles from the coastline and thereafter more steeply down to about 85 m. in a further 2–3 miles. In depths of 45–80 m. the bottom consists for the most part of muddy sand, the silt-content increasing with the depth. In over 80 m. the deposit is clay or mud.

COLLECTING METHODS

On the shore all likely habitats were searched, the amphipods found being placed in tubes and taken to the laboratory for examination. Notes were made on the spot of the abundance or otherwise of species that could be recognized, and each part of the collection was referred to the nearest tidal level.

On rocky facies the specimens were obtained by turning over stones and boulders and searching among algae. Pools were investigated and the fauna collected with a hand net. A net was used for collecting among algae at the edge of the tide. *Laminaria* holdfasts were removed complete and searched for animals in the laboratory.

Sandy beaches were investigated by sieving $\frac{1}{4}$ sq.m. samples, and by collecting specimens found under stones and among algae at low-water mark.

Particular attention was paid to fresh-water streams emptying over the beach and to the Silverburn, a small river with its estuary at Castletown.

On the offshore grounds all types of gear were used except the bottom-sampler, in particular the following: (i) naturalist's dredge with 2 ft. 6 in. mouth and a bag of heavy $\frac{1}{2}$ in. mesh; (ii) scallop dredge with 3 ft. mouth and a bag lined with shrimp netting; (iii) small otter trawl; (iv) two dredge frames, 1 ft. 6 in. and 2 ft. 6 in. across respectively, each with a bag made of sacking material; (v) D-net with canvas bag; (vi) coarse tow-net attached to the back of the otter trawl.

The first two, the naturalist's dredge and the scallop dredge, were not very successful, as part of the contents was washed out, and often only those species were obtained which were clinging to hydroids, etc., attached to stones and shells. The small otter trawl (iii) suffered from the same disadvantage and could be used only on smooth bottoms: it was useful, however, for collecting loose algae. The dredge frames with sacking (iv) were the most useful instruments. They can be used on any type of ground. They fill up almost immediately and bring up the deposit intact so that a fairly true estimate can be made of the habitat of animals found among the contents. It is necessary to attach a heavy weight to the rope a few feet in front of the dredge, and it is an advantage to have the mouth bowed out so that it will dig into the substratum. The D-net (v) was not successful: it could only be used on sand or mud and merely skimmed the surface. This may have been due to faulty construction, but its use is limited. The coarse tow-net (vi) was the most successful instrument for collecting numbers of species and individuals but it has the following disadvantages: it must be towed over a long distance and can only be used in conjunction with a trawl or dredge, and it does not provide any indication of the type of bottom over which it has travelled. It is therefore necessary to sample the deposit by other means, or to use the tow-net only on ground which is already known. The silk is easily torn on rough ground.

It is probable that a net such as that described for catching bottom plankton by Russell (1928), with slight modification to stir up the bottom, would be an excellent instrument for capturing Amphipoda, but I have had no opportunity of using it.

Wherever possible the whole of the contents of the dredge or other instrument were brought back to the laboratory and searched for amphipods. I consider it essential to adopt this procedure as it is usually impossible to look through the material thoroughly in a small boat. With the fine-meshed dredge the most satisfactory method of obtaining the specimens is to place the contents in shallow dishes with sufficient sea water just to cover them. The deposit is stirred and the dish gently tilted from side to side. Most species of amphipod are eventually caught in the surface film, though the process may take a long time. Fine sand and mud may be passed through sieves but it is difficult to sieve coarse deposits and many small forms will be missed.

The numbers of each species were recorded for each haul. The bottom deposits were occasionally analysed by sieving and weighing the separated constituents but most were graded by visual observation. Positions at sea were ascertained by means of bearings taken on prominent landmarks with a prismatic compass, and soundings were taken with a line.

A list of hauls is given in Appendix III (p. 436).

A representative collection of the species obtained is held at the Marine Biological Station, Port Erin.

The Amphipoda of the Area

There follows a systematic list of species obtained with locations and habitats. Offshore collections made during 1946 are summarized in Table I (p. 416). Under each species, where possible, a short general statement of habitat is given, compiled from my observations in conjunction with previously published work. A number of records made during 1947 from bottom-sampler hauls but not tabulated are included.

I have not included geographical range except where this is extended, as it is adequately dealt with by Chevreux & Fage (1925), Norman & Scott (1906), Stephensen (1929 and 1935–42), and Tattersall (1913).

The division of hauls into sections according to habitat in Table I was carried out from notes of the contents of the instrument used and from previous knowledge of the area. When two different types of ground were traversed in one haul, as happened with the otter trawl and tow-net, I have placed the hauls in a mixed section. Allocation to one section is sometimes arbitrary, but I have been guided by experience and any error is likely to be small.

Tidal levels are referred to by their usual abbreviations (H.W.S., H.W.N., M.T.L., L.W.N. and L.W.S.). A prefixed E. denotes 'extreme'.

Abbreviations for place-names include I.O.M. for Isle of Man, P.E. for Port Erin, and P.StM. for Port St Mary.

The terms 'shallow', 'deep', etc., as applied to the bathymetrical range of a species, refer only to the littoral system, i.e. depths of less than 200 m.

Gammaridea

LYSIANASSIDAE

Acidostoma obesum (Bate): usually in muddy sand at moderate depths. I.O.M.: 59–75 m., muddy sand, few.

Euonyx chelatus Norman: in moderately deep water; possibly always associated with *Echinus esculentus*. I.O.M.: 36–46 m., in dredge hauls with *Echinus*, few.

Nannonyx goësi Boeck: mainly at and near low-water mark among algae, and occasionally on hydroids in deeper water. I.O.M.: intertidal, in *Laminaria* holdfasts, P.StM. Ledges and Outer Harbour, few. Offshore: 60 m., on hydroids, one.

N. spinimanus Walker: no reliable estimate can be made of its habitat as the records of its occurrence are too few. I.O.M.: on *Maia squinado*, L.W.S., Langness Point, one.

Lysianassa plumosa Boeck: on coarse or mixed grounds in moderate depths. I.O.M.: 11–55 m., particularly on mixed grounds, fairly common.

Perrierella audouiniana (Bate): mainly in sponges in moderately deep water, but may occasionally be found on hydroids or algae. I.O.M.: 33–82 m., on hydroids and in sponges, few.

Orchomene humilis (Costa): usually in shallow water on algae or hydroids. I.O.M.: intertidal, in *Laminaria* holdfasts, Poyllvaaish, few. Offshore: 22–33 m., on algae and hydroids, few.

Socarnes erythrophthalmus Robertson: most abundant in fine gravel in shallow water but may also be found on fine sand. I.O.M.: intertidal: in fine sand at low water, P.E. Bay, few. Offshore: 2–18 m., in stony gravel and fine sand, abundant.

Hippomedon denticulatus (Bate): burrowing in sand of all grades, usually in fairly shallow water. I.O.M.: 9–33 m., fine and coarse sand, few.

Scopelocheirus crenatus Bate: usually on muddy sand or muddy gravel in moderate depths. Carnivorous and probably acts as a scavenger. I.O.M.: 27–82 m., particularly on muddy sand, few.

Tryphosa sarsi Bonnier: on sandy bottom in shallow water. Probably feeds on sponges and acts as a scavenger. I.O.M.: intertidal: on sponges at L.W.S., Chapel Bay, few. Offshore: 4–9 m., on muddy sand and abundant on dead fish.

Tmetonyx similis (G. O. Sars): has a wide bathymetrical distribution and seems usually to occur on mixed grounds. I.O.M.: 22–27 m., on coarse sand and broken shell, one.

Tryphosites longipes (Bate & Westwood): on muddy ground in moderate depths. I.O.M.: 68 m., muddy sand, few.

Orchomenella nana (Kröyer): commonly found on sand or mixed grounds in fairly shallow water. There are a number of records of its occurrence in dead crabs and it seems to be attracted by crustacean flesh. I.O.M.: 23–33 m., particularly on coarse sand and broken shell, fairly common.

AMPELISCIDAE

Ampelisca brevicornis (Costa): burrowing in muddy sand, usually in shallower water than the other species of the genus. I.O.M.: intertidal, in muddy sand at L.W.S., P.StM. Outer Harbour, few. Offshore: 2–18 m., fine sand, few.

A. macrocephala Lilljeborg: burrowing in mud in moderate depths. I.O.M.: 75 m., very muddy sand, one.

A. spinipes Boeck: burrowing in mixed grounds in moderate depths. Many of the records are from gravels and coarse grounds. Apparently never occurs in fine sand without mud. I.O.M.: 18–82 m., particularly in muddy sand, fairly common.

A. diadema (Costa): burrowing in muddy and mixed grounds mainly in water of moderate depth. In common with the other species of the genus it is a suspension feeder (Hunt, 1925). I.O.M.: 18–59 m., muddy sand and muddy sand with broken shell, fairly common.

A. typica (Bate): burrowing in coarse deposits usually in fairly shallow water. I.O.M.: 11–61 m., particularly in gravel and mixed grounds, few.

A. tenuicornis Lilljeborg: habitat similar to that of *A. diadema*. I.O.M.: 11–82 m., usually in muddy sand or muddy sand with broken shell, fairly common.

ARGISSIDAE

Argissa hamatipes (Norman): probably burrowing in fine or coarse deposits containing mud. I.O.M.: 15–38 m., on mixed grounds, rare.

HAUSTORIIDAE

Bathyporeia guilliamsoniana (Bate): burrowing in fine or muddy sand at L.W.S. and in shallow water. I.O.M.: intertidal, in muddy sands at L.W.S., Chapel Bay and P.StM. Outer Harbour, few. Offshore: 2–18 m., in fine sand, common.

B. elegans Watkin: burrowing in fine sand at L.W.S. and in shallow water. Its bathymetrical range is roughly the same as that of *B. guilliamsoniana* but it probably prefers cleaner sand and is usually more abundant than the latter species. I.O.M.: intertidal, in sand at L.W.S., P.E. Bay and P.StM. Outer Harbour, few. Offshore: 2–15 m., fine sand, abundant.

B. pelagica Bate: strictly intertidal, burrowing in fine sand below H.W.N. Its optimum zone is from M.T.L. to L.W.N. I.O.M.: in fine sand from H.W.N. downwards, P.E. Bay and Brewery Beach, common.

B. gracilis G. O. Sars: does not occur between tide-marks. May inhabit coarser sand than the other species in the genus and is confined to deeper water. I.O.M.: 11–35 m., mainly in coarse sand, few.

Haustorius arenarius (Slabber): usually intertidal, burrowing in sand. Its optimum zone is probably about the level of H.W.N. I.O.M.: in fine sand from H.W.N. to L.W.N., common.

Urothoë brevicornis Bate & Westwood: burrowing in fine sand from M.T.L. downwards and in shallow water. I.O.M.: not found below low-water mark. In fine sand from M.T.L. to L.W.S., P.E. Bay, few.

U. elegans Bate: usually in deeper water than *U. brevicornis* and may inhabit more muddy ground. I.O.M.: intertidal, in muddy sand at E.L.W.S., P.StM. Outer Harbour and Chapel Bay, common. Offshore: 9–60 m., particularly in sand, common.

U. marina Bate: burrows in coarser deposits than the other species of *Urothoë*, usually in coarse sand and fine gravels in moderate depths. I.O.M.: 18–37 m., particularly in coarse sand and broken shells, few.

PHOXOCEPHALIDAE

Paraphoxus oculatus G. O. Sars: probably mainly in fairly deep water, burrowing in mud or muddy sand. I.O.M.: 60 m., muddy sand, few.

Metaphoxus fultoni (T. Scott): characteristic of fine gravels, usually in rather shallow water. The animal is very small and flattened laterally and is adapted for burrowing in deposits consisting mainly of rather large particles. I.O.M.: 11–60 m., particularly in gravel, common.

Harpinia antennaria Meinert: burrowing in muddy sand, usually in fairly shallow water but may extend down to moderate depths. It is often found in company with other species of the genus, particularly *H. pectinata*. I.O.M.: intertidal, muddy sand at E.L.W.S., P.StM. Outer Harbour, fairly common. Offshore: 11–82 m., particularly in muddy sand, few.

H. pectinata G. O. Sars: burrowing in muddy sand or mud. Has not been recorded from between tide-marks. I.O.M.: 46–88 m., in muddy sand, few. In the Irish Sea it usually occurs in deeper water than *H. antennaria* but the two species overlap.

H. crenulata Boeck: burrows in mud, usually in rather deep water. I.O.M.: 59–88 m., muddy sand and mud, fairly common.

AMPHILOCHIDAE

Amphilochus manudens Bate: probably lives mainly among hydroids in moderate depths. I.O.M.: 11–37 m., particularly on hydroids and mixed grounds, fairly common.

A. spence-batei (Stebbing): perhaps usually on muddy sand but the species has been too seldom recorded for a reliable estimate to be formed. The other British records are from Torbay and Plymouth. I.O.M.: 15–18 m., on gravel and sand, rare.

Amphilochoides serratipes (Norman): on mixed ground with mud at moderate depths. I.O.M.: 27–33 m., on muddy sand with broken shell, few. The species was obtained in six hauls, all on the same type of ground.

Peltocoxa brevirostris (T. & A. Scott): on mixed grounds in moderate depths. The animal is very small, usually about 1 mm. in length, and may live interstitially. I.O.M.: 27–33 m., on mixed grounds, fairly common.

Gitana sarsi Boeck: usually in shallow water on algae and hydroids and in gravel. Occasionally occurs at low-water mark. I.O.M.: intertidal, in *Laminaria*, P.StM. Ledges, few. Offshore: 7–82 m., particularly on gravel and mixed grounds, common.

LEUCOTHOIDAE

Leucothoë spinicarpa (Abildgaard): commensal in sponges and the branchial sacs of ascidians, usually in fairly deep water but at low-water mark in suitable localities. I.O.M.: intertidal, in sponges, Poyllvaaish, few. Offshore: 60 m., in sponges, few.

L. lilljeborgi Boeck: on muddy sand or mud in which it probably burrows, as suggested by Crawford (1937*b*). I.O.M.: 11–88 m., usually on muddy ground, few.

STENOTHOIDAE

Metopa bruzelii Goës: usually associated with hydroids in fairly shallow water. I.O.M.: 18–33 m., particularly on coarse sand with broken shell, fairly common.

M. pusilla G. O. Sars: habitat similar to that of *M. bruzelii*. I.O.M.: 33–60 m., particularly on coarse sand with broken shell, few.

M. borealis G. O. Sars: habitat probably similar to that of *M. bruzelii* but it may extend into deeper water. The three species may occur together. I.O.M.: 18–82 m., particularly on mud, few.

Stenothoë monoculoides (Montagu): occurs mainly above low-water mark but may extend into shallow water. Inhabits algae and is particularly common among *Corallina* in pools from M.T.L. to L.W.N., and in *Laminaria* holdfasts at L.W.S. Occasionally found on sponges. I.O.M.: occurs throughout the area and is abundant in *Corallina* pools and in *Laminaria* holdfasts. Intertidal: P.StM. Ledges and Outer Harbour, Poyllvaaish, below Biol. Stat., Chapel Bay, Castletown Bay. Offshore: 4–18 m., on algae, few.

S. marina (Bate): usually on hydroids in fairly shallow water and occasionally on algae. I.O.M.: 11–55 m., particularly on hydroids, few.

S. antennulariae Della Valle = *S. crassicornis* Walker: probably found only on hydroids in moderately deep water, sometimes in company with *S. marina*. I.O.M.: 31–60 m., on hydroids, few.

CRESSIDAE

Cressa dubia (Bate): usually on hydroids in moderately deep water. It is fairly abundant but is probably often missed owing to its small size. I.O.M.: 22–82 m., on hydroids and mixed ground, common.

COLOMASTIGIDAE

Colomastix pusilla Grube: always associated with sponges down to moderate depths. I.O.M.: 60 m., in sponges, few.

LAPHYSTIIDAE

Laphystius sturionis Kröyer: parasitic on fish. I.O.M.: on a cod caught on a long line, many.

ACANTHONOTOZOMATIDAE

Panoploea minuta (G. O. Sars): among algae in shallow water and may extend into moderate depths on hydroids. I.O.M.: 7–64 m., on hydroids and algae, fairly common.

P. eblanae (Bate): probably on hydroids in moderately deep water. Also reported in company with *Rhizostoma*. I.O.M.: 27–60 m., on hydroids, few.

Iphimedia obesa Rathke: habitat similar to that of *Panoploea minuta* but usually occurs in rather deeper water. I.O.M.: 11–82 m., on hydroids and algae, few.

LILLJEBORGIIDAE

Lilljeborgia brevicornis Bruzelius: has a wide bathymetrical range. It is difficult to form an estimate of its habitat but it possibly occurs mainly on hydroids. I.O.M.: 60 m., on hydroids, few.

L. kinahani (Bate): on fine gravels and mixed grounds in fairly shallow water. I.O.M.: 11–55 m., on gravel and mixed grounds, common.

OEDICEROTIDAE

Perioculodes longimanus (Bate & Westwood): burrowing in fine or muddy sand at L.W.S. and in shallow water. Occasionally extends into moderate depths. I.O.M.: intertidal, in muddy sand at extreme L.W.S., P.StM. Outer Harbour and Chapel Bay, fairly common. Offshore: 4–82 m., fine and muddy sand, common.

Pontocrates arenarius (Bate): burrows in fine sand preferably without mud from M.T.L. to a depth of a few metres. Its main centre of distribution is about L.W.S. I.O.M.: intertidal, in fine sand from M.T.L. downwards, P.E. Bay and Chapel Bay, fairly common. Offshore: 2–11 m., fine sand, few.

P. norvegicus Boeck: burrows in fine or muddy sand from M.T.L. to shallow water. I.O.M.: more abundant in shallow water than between tide-marks. Extends into rather deeper water than *P. arenarius* and will burrow in muddy sand, whereas *P. arenarius* prefers clean sand. Intertidal: in fine and muddy sand, from M.T.L. downwards, P.E. Bay, P.StM. Outer Harbour, and Chapel Bay, few. Offshore: 2–18 m., fine sand, common.

Synchelidium haplocheles Grube: in fairly shallow water but usually at a greater depth than the species of *Pontocrates*. Burrows in a wide range of deposits from fine sand to gravel. I.O.M.: 4–35 m., in fine sand, gravel and mixed grounds, fairly common.

Monoculodes carinatus Bate: usually in fairly shallow water and probably burrows mainly in rather coarse deposits. I.O.M.: 11–33 m., mixed grounds, few.

M. subnudus Norman: habitat similar to that of *M. carinatus* but may occur in deeper water. I.O.M.: 7–33 m., mixed grounds, few.

Westwoodilla caecula (Bate): in mud or muddy sand usually in fairly deep water. I.O.M.: 82 m., mud, fairly common.

TIRONIDAE

Syrrhoites fimbriatus (Stebbing & Robertson): probably mainly on mixed grounds in moderately deep water. This species has only once been found outside the Irish Sea and the Firth of Clyde, but as this record was from north of Spitsbergen it must have a much wider geographical range than would appear from the few published finds. It has probably been missed largely because of its minute size. I.O.M.: 11–55 m., mixed grounds, few.

CALLIOPIIDAE

Calliopius crenulatus Chevreux & Fage: mainly on algae near low-water mark. I.O.M.: on sand at extreme L.W.S., P.E. Bay, few.

Apherusa cirrus (Bate): near or just below low-water mark on algae. I.O.M.: occurs particularly on *Halidrys siliquosa* with which it tones so well that it is difficult to distinguish. At L.W.S., Chapel Bay, Castletown Bay, Niarbyl, common.

A. bispinosa (Bate): usually on algae in shallow water and between tide-marks in pools and sheltered situations, but it may extend into fairly deep water where it probably lives on hydroids. I.O.M.: intertidal, in *Laminaria* holdfasts, on *Halidrys* and red algae at low-water mark, P.StM. Ledges and Outer Harbour, Chapel Bay, Castletown Bay, Poyllvaaish, few. Offshore: 2–59 m., mainly on algae and fine gravel, common.

A. jurinei (Milne-Edwards): among algae between tide-marks, only occasionally occurring offshore. Found in *Corallina* and *Enteromorpha* pools from H.W.N. downwards. Particularly common in the holdfasts of *Laminaria digitata*. I.O.M.: occurs throughout the area but is more abundant on exposed situations on rock. In sheltered places it is largely replaced by *Apherusa bispinosa*. Exhibits a large number of colour varieties. Intertidal: P.StM. Ledges and Inner Harbour, Poyllvaaish, Niarbyl, below Biol. Stat., Spaldrick, Chapel Bay, Castletown Bay. Offshore: 9–31 m., on algae, few.

PLEUSTIDAE

Parapleustes monocuspis (G. O. Sars): on hydroids in moderate depths. I.O.M.: 33–37 m., on hydroids, few. This species has not previously been recorded from the Irish Sea, but Walker (1895) stated that he had collected specimens on the north coast of Wales corresponding to this form, which he regarded as the young of *P. bicuspis*. He had constantly collected the two forms together and observed that only the largest specimens had a dorsal tooth on the first pleon segment, and this varied in length in proportion to the size of the specimen. It seems clear, however, from the descriptions of Sars (1895), that the two species are really distinct.

Stenopleustes nodifer (G. O. Sars): on mixed grounds and hydroids in fairly deep water. I.O.M.: 29–82 m., on mixed grounds and hydroids, few.

PARAMPHITHOIDAE

Epimeria cornigera (J. C. Fabricius): on coarse ground and particularly on corals in rather deep water. I.O.M.: 55–84 m., mud and coarse sand with broken shell, few.

ATYLIDAE

Nototropis swammerdami (Milne-Edwards): among algae on sandy bottoms in very shallow water and occasionally above low-water mark on sandy shores. I.O.M.: intertidal, on sand and among weed at L.W.S. P.E. Bay, Chapel Bay, Castletown Bay, fairly common. Offshore: 2–15 m., among weed on sand, common.

N. vedlomensis (Bate & Westwood): on mixed grounds and gravels, usually in deeper water than *N. swammerdami*. Conceals itself in the deposit in the manner described by Crawford (1937*b*) for *Maera othonis*. I.O.M.: 7–60 m., on gravel and mixed grounds, common.

MELPHIDIPPIDAE

Melphidippella macra (Norman): habitat similar to that of *Nototropis vedlomensis*. The two species often occur in the same hauls. I.O.M.: 9–82 m., mainly on mixed grounds, common.

EUSIRIDAE

Eusirus longipes Boeck: usually on mixed or muddy grounds in moderate depths. I.O.M.: 11–60 m., mainly on mixed grounds, fairly common.

GAMMARIDAE

Gammarellus homari (J. C. Fabricius): among algae in shallow water and at low-water mark. I.O.M.: intertidal, among *Laminaria* at low-water mark and on floating buoy, P.StM. Ledges, Niarbyl, P.E. Breakwater, common. Offshore: 1–18 m., on weed, few. The specimens from P.StM. included a number of adults of the form *homari* while those from P.E. Bay were all of the form *angulosus*. I am unable to detect any morphological difference between the two forms other than the length of the projections of the dorsal carina, and therefore treat them as belonging to one species. At the same time the collections included ovigerous females about 10 mm. in length of both forms.

Cheirocratus sundevalli (Rathke): mainly on mixed grounds and gravels in moderate depths. Also occurs occasionally on loose weed. I.O.M.: 9–37 m., in gravel and mixed grounds, fairly common.

C. intermedius G. O. Sars, probably on muddy grounds in moderate depths. I.O.M.: 66–84 m., in muddy sand, few.

C. assimilis Lilljeborg: habitat similar to that of *C. sundevalli*, but usually less abundant. I.O.M.: 27 m., mixed grounds, few.

Megaluropus agilis Hoek: burrowing in fine sand in shallow water. Also occurs on loose weed. I.O.M.: 2–15 m., in fine sand and on weed, common.

Melita pellucida G. O. Sars: among decaying vegetation in slightly brackish water of salinity up to about 3 $^{0}/_{00}$. I.O.M.: upper part of Silverburn estuary, few.

M. palmata (Montagu): under stones and on algae mainly from M.T.L. to L.W.N. Can tolerate reduction in salinity down to about 13 $^{0}/_{00}$ and penetrates some distance into estuaries. I.O.M.: under stones from M.T.L. to L.W.S., P.StM. Ledges and Inner Harbour, Chapel Bay, Spaldrick, Brewery Beach, lower part of Silverburn, Niarbyl, fairly common.

M. hergensis Reid: habitat similar to that of *M. palmata* but probably does not penetrate estuaries and occurs from above L.W.S. to shallow water. I.O.M.: intertidal, under stones on sand at L.W.S., Chapel Bay, common. Offshore: 2–22 m., on weed on sand, few.

M. obtusata (Montagu): on sublittoral algae and occasionally at low-water mark, and also on *Asterias rubens* and *Luidia ciliaris* in deeper water. The specimens from echinoderms are coloured white, while those from algae are brown or dark coloured.

I.O.M.: intertidal, on algae at L.W.S., P.E. Bay, Chapel Bay, P.StM. Inner Harbour, few. Offshore: 11–33 m., mainly on *Asterias* and *Luidia*, common.

Ceradocus semiserratus (Bate): in fine gravels and mixed grounds usually in fairly shallow water. I.O.M.: 11–55 m., on gravel and coarse sand with broken shell, common.

Maera othonis (Milne-Edwards): usually on coarse deposits mixed with fine or muddy sand in moderate depths. Occasionally at L.W.S. It shelters under pieces of shell and pebbles. I.O.M.: the most widely distributed amphipod on the offshore grounds of the area. It occurs on most types of bottom but is most abundant on mixed grounds and gravel. Intertidal: 7–82 m., gravel, mixed grounds, and hydroids, common.

Maerella tenuimana (Bate): appears to occur only in coarse sand deposits in moderate depths and to be absent from ground containing mud. Probably burrows in the substratum. I.O.M.: 22–35 m., in coarse sand and coarse sand with broken shell, few.

Gammarus locusta (L.): typically a marine species occurring on sandy ground beneath stones and among algae usually at low-water mark and in shallow water. Can tolerate some reduction in salinity and normally penetrates for a short distance up estuaries. In certain parts of its range *G. locusta* may live in salinities down to as low as 5–6 $^{\circ}/_{oo}$. (See Spooner, 1947, and Segerstråle, 1947.) I.O.M.: intertidal, under stones on sand at low water, P.E. Bay, P.StM. Inner Harbour, Chapel Bay, Poyllvaaish, Castletown Bay, abundant. Offshore: 0–18 m., weed on sand, particularly abundant near water's edge. In the area it is only found in fully marine conditions. Young individuals may occur higher up the shore than the adults.

G. zaddachi Sexton subsp. *zaddachi* Spooner 1947: inhabits the upper end of estuaries (roughly about the top third of the estuarine zone) and brackish water of low salinities. In some areas can maintain itself under pure fresh-water conditions (Spooner, 1947). I.O.M.: occurs only in the Silverburn from the overlap zone with *G. z. salinus* to the upper limit of salt-water penetration, where the water is entirely fresh except for short periods at H.W.S.

G. zaddachi Sexton subsp. *salinus* Spooner 1947: inhabits the middle reaches of stuaries where the salinity fluctuation is greatest; mingling with *G. locusta* at the seaward end, and with *G. z. zaddachi* towards the river end. Cannot tolerate fresh water (Spooner, 1947). I.O.M.: occurs in all streams which run into the sea over sandy shores, from L.W.N. to about M.T.L. It is absent from streams which run their entire course over rocks and through boulders. Also occurs in the Silverburn in weed and under stones in the stream from the harbour mouth to the limit of high salinity at high tide where it overlaps with *G. z. salinus*.

G. duebeni Lilljeborg: in brackish and fresh water on the upper part of the shore, in estuaries, and in small streams. Under stones, in rock pools, and among algae and fresh-water vegetation. Occurs in water of salinity up to about 21 $^{\circ}/_{oo}$ but usually lower than this value, and is very resistant to unfavourable conditions (Segerstråle, 1946). I.O.M.: occurs from H.W.N. to H.W.S. in streams which flow over rock and shingle into the sea, and in brackish pools above high-water mark. It is also found in some small fresh-water streams up to a considerable height above sea-level. These streams are reduced to mere trickles in times of drought. In other larger streams it was not found above high-water mark. Found with *G. pulex* only in the Silverburn. Presumably the animals occurring on the shore belong to Reid's type α, while those found in streams are of type β (Reid, 1939). Localities: Spaldrick, P.E. Bay, Brewery Beach, common.

G. pulex (L.): among vegetation and under stones in fresh-water streams and lakes. Cannot tolerate increased salinity. It is apparently commoner in hard than in soft water. I.O.M.: occurs only in the Silverburn above the tidal zone.

Marinogammarus marinus (Leach): strictly intertidal, optimum between H.W.N. and M.T.L. Under stones, in fucoids, on gravel, mixed grounds, and soft mud, but absent or scarce on cleaner sands or shingle. Penetrates estuaries for some distance, and can tolerate salinities down to about $10\,^{\circ}/_{00}$. I.O.M.: occurs on all rocky shores and is sometimes very abundant. Only found below M.T.L. where there is fresh-water influence. Occurs in streams where it is subject to considerable salinity changes and spends the greater part of each day in water which is entirely fresh. Localities: P.StM. Ledges and Outer Harbour, Spaldrick, Niarbyl, Poyllvaaish, Brewery Beach, Castletown Bay, lower part of Silverburn estuary.

M. obtusatus (Dahl): essentially intertidal, optimum about M.T.L. to L.W.N. Under stones and seaweed. Associated with less muddy and more stony grounds, and capable of existing on comparatively clean pebbles. Penetrates only a short distance into estuaries. Probably cannot tolerate salinities below about $33{\cdot}5\,^{\circ}/_{00}$ except for short periods. I.O.M.: occurs on all rocky shores. Found sparingly in fresh-water streams running over the beach. Intertidal: P.StM. Ledges and Outer Harbour, Spaldrick, Niarbyl, Poyllvaaish, Brewery Beach, Castletown Bay, abundant. Offshore: 9–5 m. in weed on gravel, one.

M. finmarchicus (Dahl): habitat similar to that of *M. obtusatus* but more local and never so abundant. Possibly a tendency to inhabit situations which remain wet at low tide. I.O.M.: Spaldrick, below Biol. Stat., Bradda Head, locally common.

M. stoerensis Reid: strictly intertidal between H.W.N. and L.W.N. where fresh-water streams or seepage flow over the tidal zone. Under flat stones. Penetrating only a short distance into estuaries. Apparently this species can only exist where there are large periodical changes in salinity. I.O.M.: under stones in fresh-water streams, Spaldrick, Brewery Beach, lower part of Silverburn, common.

M. pirloti Sexton & Spooner: between H.W.N. and L.W.N. on stony beaches where there is fresh-water influence. I.O.M.: occurs in streams running over reefs or pebbles and emptying into the sea over sand. Its optimum zone is from H.W.N. to M.T.L. Occasional specimens may apparently occur away from fresh-water influence, as one individual was obtained from *Fucus serratus* at L.W.S., in company with *Gammarus locusta*. Brewery Beach, abundant.

Pectenogammarus planicrurus Reid: the records are too few to formulate a general idea of its habitat, but apparently it is usually intertidal and occurs under boulders (Reid, 1944). I.O.M.: under stones between H.W.N. and L.W.N., Spaldrick, few.

DEXAMINIDAE

Dexamine spinosa (Montagu): among algae at low-water mark and in shallow water. I.O.M.: intertidal, among algae at L.W.S., Chapel Bay and Castletown Bay, few. Offshore: 4–22 m., among weed on sand and gravel, common.

D. thea Boeck: among algae. A more pronounced littoral form than *D. spinosa* but also found in shallow water. I.O.M.: occurs in sheltered situations particularly among *Laminaria* at L.W.S. Intertidal: P.StM. Outer Harbour, below Biol. Stat., Chapel Bay, Castletown Bay, locally common. Offshore: 7–18 m., weed on sand and gravel, few.

Tritaeta gibbosa (Bate): among algae and associated with sponges usually at low-water mark but sometimes extending into fairly deep water. I.O.M.: intertidal, in sponges and *Laminaria* holdfasts at low-water mark, P.StM. Ledges, below Biol. Stat., Chapel Bay, Poyllvaaish, Niarbyl, fairly common. Offshore: 15–60 m., among algae and on sponges, few.

Guernea coalita (Norman): on coarse or mixed grounds in fairly shallow water where it probably lives interstitially. I.O.M.: 11–33 m., in coarse sand and mixed grounds, fairly common.

TALITRIDAE

Talitrus saltator (Montagu): burrowing into loose sand and beneath rotting weed on sandy beaches at H.W.S. In the winter months they are found some distance below the surface and possibly hibernate in the manner described for *Talorchestia megalophthalma* by Edwards & Irving (1943). I.O.M.: in loose sand at H.W.S., P.E. Bay, abundant.

Orchestia mediterranea A. Costa: usually under stones at about H.W.N. Occupies a zone distinctly below that of *O. gammarella*, though the two species overlap. Usually found with *Marinogammarus marinus*. I.O.M.: under stones at H.W.N., Niarbyl, Poyllvaaish, abundant.

O. gammarella (Pallas): usually on rocky shores at and above H.W.S. under stones and among rotting algae. In damp places it may extend considerably above sea-level. I.O.M.: abundant on all shingle beaches beneath rotting weed at H.W.S., P.StM. Outer Harbour, Spaldrick, Poyllvaaish, Niarbyl, Castletown Bay.

Talorchestia deshayesei (Audouin): under rotting weed and stones on sand at H.W.S. I.O.M.: very local and was not collected with *Talitrus*, although the habitats of the two species are very similar. Castletown Bay, Derby Haven.

Hyale prevosti (Milne-Edwards) = *H. nilssoni* (Rathke): among algae, usually between H.W.N. and L.W.N. Can tolerate fresh water for some time and penetrates estuaries. I.O.M.: occurs on all rocky shores. It lives over most of the tidal zone, being common in *Pelvetia* at H.W.N. and among algae in pools down to L.W.N. It is found more rarely in *Laminaria* holdfasts and red algae at L.W.S. and occasionally offshore in a few metres depth. Intertidal: P.StM. Ledges, Spaldrick, below Biol. Stat., Niarbyl, Brewery Beach, Castletown Bay, lower part of Silverburn. Offshore: 9–15 m., one.

H. pontica (Rathke): among algae near L.W.S., usually in rather exposed situations. I.O.M.: occurs only among algae from L.W.S. and on a floating buoy. Was not found offshore. In one collection it occurred in company with *H. prevosti* at L.W.S. but was considerably more abundant. P.E. Breakwater, fairly common.

AORIDAE

Aora typica Kröyer: on algae and hydroids in fairly shallow water and occasionally at L.W.S. in sheltered situations. I.O.M.: intertidal in *Laminaria* holdfasts, P.StM. Outer Harbour, below Biol. Stat., Castletown Bay, few. Offshore: 11–33 m., on algae and hydroids, common.

Microdeutopus damnoniensis (Bate): among algae at low-tide mark and in very shallow water. I.O.M.: on muddy sands at L.W.S., P.StM. Inner Harbour, and Chapel Bay, few.

Lembos websteri Bate: at L.W.S. and in shallow water on algae, particularly in the holdfasts of *Laminaria digitata*. I.O.M.: intertidal, abundant everywhere in *Laminaria* holdfasts, P.StM. Ledges and Outer Harbour, below Biol. Stat., Chapel Bay, Poyllvaaish, Castletown Bay, Niarbyl. Offshore: 7–22 m., on algae, few.

L. longipes (Lilljeborg): burrowing in coarse to muddy sand in moderate depths. I.O.M.: 29–82 m., in coarse and muddy sand, fairly common.

PHOTIDAE

Microprotopus maculatus Norman: always associated with a sandy bottom in shallow water. May sometimes burrow into the deposit but its usual habitat is among loose algae. I.O.M.: 2–18 m., in weed on sand, common.

Photis longicaudata (Bate & Westwood): probably burrows in fine to muddy sand or mixed grounds in moderate depths. I.O.M.: 27–82 m., on mixed grounds, few.

Eurystheus melanops (G. O. Sars): probably on mixed grounds in moderately deep water. I.O.M.: 11–33 m., mixed grounds, few. This species has not previously been recorded with certainty from the British Isles as there has been some confusion with *E. erythrophthalmus*. It is much scarcer than the next species.

E. erythrophthalmus (Lilljeborg) = *E. maculatus* (Johnston): usually on hydroids in moderate depths and on algae in shallow water. Between tide-marks it seems to be almost confined to the holdfasts of *Laminaria digitata*, of which it is a typical and sometimes abundant inhabitant. I.O.M.: intertidal, in *Laminaria* at low-water mark, P.StM. Ledges, below Biol. Stat., Poyllvaaish, Castletown Bay, Niarbyl, common. Offshore: 2–82 m., mainly on hydroids and algae, common.

E. palmatus (Stebbing & Robertson): on hydroids and muddy or mixed grounds in fairly deep water. I.O.M.: 29–60 m., on hydroids and mixed grounds, few.

Podoceropsis nitida Stimpson: in moderately deep water on hydroids or commensal in the shells inhabited by hermit crabs. I.O.M.: 11–60 m., in shells of *Buccinum* inhabited by *Eupagurus bernhardus* and on hydroids, common.

Megamphopus cornutus Norman: in mixed grounds usually in fairly shallow water. I.O.M.: 7–33 m., on mixed grounds, fairly common.

Protomedeia fasciata Kröyer: in muddy sand at moderate depths. I.O.M.: 73 m., muddy sand, few. Not previously obtained so far south.

Leptocheirus hirsutimanus Bate: probably in rather coarse or mixed grounds in moderate depths. I.O.M.: 33 m., mixed grounds, few.

L. pectinatus Norman: in fine gravel or mixed grounds, usually in fairly shallow water. I.O.M.: 9–36 m., in gravel and mixed grounds, common.

ISAEIDAE

Isaea montagui Milne-Edwards: only found on the mouthparts of *Maia squinado*. I.O.M.: on *Maia*, Langness Point, few.

AMPHITHOIDAE

Amphithoë rubricata (Montagu): on the shore or in shallow water on algae or under stones. Occurs in pools and among algae from M.T.L. downwards, and is particularly abundant in the holdfasts of *Laminaria digitata*. I.O.M.: intertidal, under stones and in *Laminaria* holdfasts, P.StM. Ledges and Outer Harbour, below Biol. Stat., Chapel Bay, Poyllvaaish, Castletown Bay, common. Offshore: 7–18 m., on algae, few.

Pleonexes gammaroides Bate: habitat similar to that of *Amphithoë rubricata* but favours more exposed positions. I.O.M.: intertidal, among algae at L.W.S., P.StM. Ledges, Chapel Bay, P.E. Breakwater, few. Offshore: 7–15 m., on algae, one.

Sunamphithoë pelagica (Milne-Edwards): usually on algae in shallow water. I.O.M.: intertidal, on *Fucus* at L.W.S., P.StM. Inner Harbour, one. Offshore: 4–9 m., on algae, one.

Biancolina cuniculus (Stebbing): probably among algae in very shallow water. I.O.M.: on red algae at extreme L.W.S., Chapel Bay, one. Not previously recorded farther north than Devon. Apparently very rare.

JASSIDAE

Jassa falcata (Montagu) incl. *J. dentex* (Czerniavski), Chevreux & Fage (1925, p. 348): among algae at low-water mark and in very shallow water. Particularly abundant and grows to a large size among the algae on floating buoys. The younger forms are sometimes found in sponges. On the authority of Mrs E. W. Sexton (*in litt.*) I have included the form described by Chevreux & Fage as *J. dentex* (Czerniavski) in the species *J. falcata* (Montagu). Both forms of the male are common in the area and sometimes occur together. This was noted by Walker (1911). I.O.M.: intertidal, in *Laminaria* holdfasts and occasionally on sponges at L.W.S., P.StM. Ledges and Outer Harbour, below Biol. Stat., P.E. Breakwater and buoy, Poyllvaaish, Castletown Bay, Niarbyl, common. Offshore: 2–15 m., on algae, few.

J. pusilla (G. O. Sars): on hydroids and among sponges on *Inachus dorsettensis* in moderately deep to deep water. Apparently never in very shallow water. I.O.M.: 27–33 m., on *Inachus*, common.

J. ocia (Bate): among algae and particularly in sponges from M.T.L. to L.W.S. I.O.M.: in sponges and *Laminaria* holdfasts on the shore from M.T.L. downwards, P.StM. Ledges, below Biol. Stat., Poyllvaaish, Castletown Bay, fairly common.

Parajassa pelagica (Leach): habitat similar to that of *Jassa falcata* but generally scarcer. I.O.M.: among algae at L.W.S., P.StM. Ledges, P.E. Breakwater and buoy, Poyllvaaish, Niarbyl, few.

Microjassa cumbrensis (Stebbing & Robertson): mainly on mixed grounds in moderately deep water. It may live interstitially or on hydroids. I.O.M.: 11–64 m., on mixed grounds and hydroids, fairly common.

COROPHIIDAE

Ericthonius brasiliensis (Dana): on algae at L.W.S. in sheltered situations and extending into deeper water on hydroids. I.O.M.: intertidal, in *Laminaria* holdfasts, P.StM. Inner and Outer Harbours, Poyllvaaish, few. Offshore: 1–82 m., on algae and hydroids, fairly common.

Unciola planipes Norman: probably burrowing in coarse sand or mixed grounds, usually in fairly deep water. I.O.M.: 35 m., in coarse sand, few.

Siphonoecetes dellavallei Stebbing: on fine sand in shallow water living in tubes constructed of sand grains and fine gravel usually attached to small pieces of shell. I.O.M.: 2–18 m., on fine sand, common.

Corophium volutator (Pallas): burrowing in muddy sand in sheltered places between tide-marks on the shore, but usually in estuaries. It is found in varying salinity conditions from about 1 to 34 $^{\circ}/_{\circ\circ}$. The controlling factor in its distribution is probably the presence or absence of a suitable soil which depends largely on the amount of shelter from winds and currents (Hart, 1930; Beanland, 1940). I.O.M.: in muddy sand from H.W.N. to M.T.L., P.StM. Inner Harbour and Silverburn Estuary, abundant. The species seems to be absent or very scarce in P.StM. Inner Harbour during the early part of the year. At least it could not be found there at the end of March 1946, but was abundant a month later, and the population then included many large ovigerous females. It is possible that in this locality it is a summer visitor (see Beanland, 1940).

C. affine Bruzelius: burrowing in muddy sand, usually in moderately deep water. I.O.M.: 59 m., muddy sand, fairly common.

C. crassicorne Bruzelius: burrowing in muddy sand in shallow water and at L.W.S. in sheltered situations. I.O.M.: in muddy sand at E.L.W.S., P.StM. Outer Harbour, few.

C. bonelli (Milne-Edwards): in tubes on algae and hydroids at L.W.S. and in fairly shallow water. I.O.M.: intertidal, in *Laminaria* holdfasts and on sponges, P.StM. Outer Harbour, below Biol. Stat., Chapel Bay, Poyllvaaish, Niarbyl, few. Offshore: 11–27 m., on algae and hydroids, few.

CHELURIDAE

Chelura terebrans Philippi: bores in wooden piles, etc., and in submerged driftwood in shallow water. I.O.M.: in submerged wood, 18 m., abundant.

PODOCERIDAE

Dulichia porrecta (Bate): in moderately deep water. The type of ground that it usually inhabits is difficult to estimate from the records. It may be often associated with *Pecten maximus* on mixed grounds. I.O.M.: 29 m., on muddy sand with broken shell, one.

Caprellidea

CAPRELLIDAE

Phtisica marina Slabber: usually on algae or hydroids from L.W.S. to fairly deep water. I.O.M.: intertidal, in mud in deep clefts at L.W.S., P.StM. Ledges, few. Offshore: 2–82 m., on algae, hydroids, and mixed grounds, common.

Pseudoprotella phasma (Montagu): on algae and hydroids at L.W.M. and in fairly shallow water, sometimes descending to greater depths. I.O.M.: 7–33 m., on algae and hydroids, common. It is particularly common on *Obelia* growing on the fronds of *Laminaria*.

Podalirius typicus Kröyer = *Pariambus typicus* (Kröyer): usually in fairly shallow water on fine sand or in the ambulacral grooves of *Asterias* or *Solaster*. I.O.M.: intertidal, muddy sand at L.W.S., P.StM. Outer Harbour, one. Offshore: 4–29 m., mainly on fine sand, fairly common.

Parvipalpus capillaceus (Chevreux): habitat impossible to estimate. I.O.M.: 29 m., muddy sand with broken shell, one. Apparently a very rare species, being known previously only from the west coast of France and Valencia Harbour, Eire.

Caprella acanthifera Leach: from L.W.N. to shallow water offshore, mainly on algae and sponges, seldom on hydroids. I.O.M.: intertidal, in *Laminaria* holdfasts and on sponges under stones from L.W.N. downwards, P.StM. Ledges and Outer Harbour, Chapel Bay, Castletown Bay, Niarbyl, few. Abundant at Poyllvaaish. Offshore: 4–29 m., on algae, common.

C. acutifrons Latreille: on floating wreckage, buoys, and breakwater. In deep water on sponges and hydroids. Sometimes associated with tunicates (Harrison, 1944). I.O.M.: on red algae at L.W.S., P.E. Breakwater, common.

C. linearis (L.): on hydroids and floating wreckage, buoys, etc. Usually below low-water mark but intertidally in suitable localities. I.O.M.: intertidal, on red algae at L.W.S., P.E. Breakwater, few. Offshore: 11–37 m., on hydroids and algae, locally common.

C. fretensis Stebbing: probably on algae and hydroids in fairly shallow water. I.O.M.: intertidal, on red algae at L.W.S., P.E. Breakwater, one. Offshore: 11–18 m., on algae, one. Previously known only from the Channel and farther south.

Hyperiidea

HYPERIIDAE

Hyperia galba (Montagu): at or near the surface, usually commensal with Scyphomedusae. I.O.M.: commensal with *Rhizostoma*, common.

Themisto abyssorum (Boeck) = *Parathemisto oblivia* (Kröyer): pelagic usually in deep water, sometimes near surface. I.O.M.: 82 m., in young fish trawl, one.

DISCUSSION

Economic Importance

The most striking fact that emerges from intensive collecting of amphipods is that of their general abundance. On the shore species of *Marinogammarus* or *Bathyporeia*, on rocky or sandy facies respectively, are often present in large numbers and sometimes extremely plentiful. Near low-water mark a variety of species are very common among algae. It is, however, in moderate depths that the group reaches its maximum importance. In shallow water it is no uncommon occurrence to obtain several hundred individuals in a short haul.

TABLE I. THE DISTRIBUTION OF THE OFFSHORE SPECIES

(The figures opposite each species give the total number captured on each type of ground or habitat)

Type of ground or habitat ...	Algae	Fine sand (and algae)	Sand and gravel with algae	Stony gravel	Coarse sand	Coarse sand and broken shell	Hydroids	Muddy sand and broken shell	Muddy sand	Mud	Sponges
Number of hauls	10	12	11	4	3	12	11	17	6	3	2
Lysianassidae:											
Acidostoma obesum	—	—	—	—	—	—	—	—	1	—	—
Euonyx chelatus	—	—	—	—	—	—	1	—	—	—	—
Nannonyx goësi	—	—	—	—	—	—	1	—	—	—	—
Lysianassa plumosa	—	—	3	—	—	11	3	16	1	—	—
Perrierella audouiniana	—	—	—	—	—	—	2	—	—	—	23
Orchomene humilis	2	—	—	—	—	—	8	—	—	—	—
Socarnes erythrophthalmus	—	13	296	95	—	—	—	—	—	—	—
Hippomedon denticulatus	—	1	—	—	1	—	—	—	—	—	—
Scopelocheirus crenatus	—	—	—	—	—	1	1	3	6	1	—
Tryphosa sarsi	—	3	—	—	—	—	—	—	—	—	—
Tmetonyx similis	—	—	—	—	—	1	—	—	—	—	—
Orchomenella nana	4	—	—	—	—	51	—	6	—	—	—
Ampeliscidae:											
Ampelisca brevicornis	—	9	2	—	—	—	—	—	—	—	—
A. spinipes	—	—	2	1	—	6	1	18	21	—	—
A. diadema	—	—	2	—	—	7	1	31	18	—	—
A. typica	—	—	8	2	—	5	—	3	1	—	—
A. tenuicornis	—	—	—	1	—	7	—	31	30	1	—
Argissidae:											
Argissa hamatipes	—	—	1	—	—	—	—	1	—	—	—
Haustoriidae:											
Bathyporeia guilliamsoniana	—	51	5	—	—	—	—	—	—	—	—
B. elegans	—	336	52	—	—	—	—	—	—	—	—
B. gracilis	—	1	—	2	7	2	—	1	—	—	—
Urothoë elegans	—	11	60	—	—	4	—	5	4	—	—
U. marina	—	—	—	—	1	12	1	1	—	—	—
Phoxocephalidae:											
Paraphoxus oculatus	—	—	—	—	—	—	—	—	2	—	—
Metaphoxus fultoni	—	2	48	40	—	19	—	12	1	—	—
Harpinia antennaria	—	16	—	—	—	1	—	4	3	—	—
H. pectinata	—	—	—	—	—	3	—	—	19	1	—
H. crenulata	—	—	—	—	—	—	—	—	25	6	—
Amphilochidae:											
Amphilochus manudens	1	—	3	—	—	14	14	16	—	—	—
A. spence-batei	—	—	2	—	—	—	—	—	—	—	—
Amphilochoides serratipes	—	—	—	—	—	—	—	9	—	—	—
Peltocoxa brevirostris	—	—	—	—	—	15	1	17	—	—	—
Gitana sarsi	1	—	86	6	—	5	6	19	—	—	—
Leucothoidae:											
Leucothoë spinicarpa	—	—	—	—	—	—	3	—	—	—	4
L. lilljeborgi	—	—	2	—	—	—	—	2	1	1	—
Stenothoidae:											
Metopa bruzelii	—	—	—	—	—	17	2	7	—	—	—
M. pusilla	—	—	—	—	—	4	1	1	—	—	—
M. borealis	—	—	—	—	—	2	1	2	—	4	—
Stenothoë monoculoides	3	—	3	—	—	—	—	—	—	—	—
S. marina	3	3	3	—	—	—	10	—	1	—	—
S. antennulariae	—	—	—	—	—	4	18	1	—	—	—

Table I (*cont.*)

Type of ground or habitat...	Algae	Fine sand (and algae)	Sand and gravel with algae	Stony gravel	Coarse sand	Coarse sand and broken shell	Hydroids	Muddy sand and broken shell	Muddy sand	Mud	Sponges
Number of hauls	10	12	11	4	3	12	11	17	6	3	2
Cressidae:											
Cressa dubia	1	—	—	—	—	66	90	61	—	—	—
Colomastigidae:											
Colomastix pusilla	—	—	—	—	—	—	—	—	—	—	5
Acanthonotozomatidae:											
Panoploea minuta	5	—	7	—	—	2	25	1	—	—	—
P. eblanae	—	—	—	—	—	—	3	2	—	—	—
Iphimedia obesa	1	—	—	—	—	1	1	—	—	1	—
Lilljeborgiidae:											
Lilljeborgia brevicornis	—	—	—	—	—	—	4	—	—	—	—
L. kinahani	—	1	39	4	—	48	9	7	—	—	—
Oedicerotidae:											
Perioculodes longimanus	1	40	22	—	—	—	—	—	9	7	—
Pontocrates arenarius	—	26	—	—	—	—	—	—	—	—	—
P. norvegicus	2	103	14	—	—	—	—	—	—	—	—
Synchelidium haplocheles	—	10	28	3	1	16	2	25	—	—	—
Monoculodes carinatus	—	—	4	—	—	4	—	6	—	—	—
M. subnudus	—	1	2	—	—	1	—	7	—	—	—
Westwoodilla caecula	—	—	—	—	—	—	—	—	—	53	—
Tironidae:											
Syrrhoites fimbriatus	—	—	5	—	—	5	—	1	—	—	—
Calliopiidae:											
Apherusa bispinosa	31	30	263	2	—	—	2	4	3	—	—
A. jurinei	—	3	2	—	—	—	—	1	—	—	—
Pleustidae:											
Parapleustes monocuspis	—	—	—	—	—	—	10	—	—	—	—
Stenopleustes nodifer	—	—	—	—	—	11	4	7	—	—	—
Paramphithoidae:											
Epimeria cornigera	—	—	—	—	—	2	—	—	—	1	—
Atylidae:											
Nototropis swammerdami	56	4	—	—	—	—	—	—	—	—	—
N. vedlomensis	—	2	9	12	—	19	—	30	1	—	—
Melphidippidae:											
Melphidippella macra	—	1	3	—	—	16	3	36	3	—	—
Eusiridae:											
Eusirus longipes	—	—	1	—	—	16	4	6	1	—	—
Gammaridae:											
Gammarellus homari	—	1	1	—	—	—	—	—	—	—	—
Cheirocratus sundevalli	—	—	13	1	—	10	—	11	1	—	—
C. assimilis	—	—	—	—	—	5	—	2	—	—	—
Megaluropus agilis	—	94	12	—	—	—	—	—	—	—	—
Melita hergensis	1	2	2	—	—	—	—	—	—	—	—
M. obtusata	1	—	2	—	—	—	—	1	—	—	—
Ceradocus semiserratus	2	—	200	24	—	13	1	2	—	—	—
Maera othonis	1	2	13	3	—	58	17	38	2	—	—
Maerella tenuimana	—	—	—	—	4	4	—	—	—	—	—
Gammarus locusta	1	8	8	—	—	—	—	—	—	—	—
Marinogammarus obtusatus	—	—	1	—	—	—	—	—	—	—	—

Table I (*cont.*)

Type of ground or habitat ...	Algae	Fine sand (and algae)	Sand and gravel with algae	Stony gravel	Coarse sand	Coarse sand and broken shell	Hydroids	Muddy sand and broken shell	Muddy sand	Mud	Sponges
Number of hauls	10	12	11	4	3	12	11	17	6	3	2
Dexaminidae:											
Dexamine spinosa	52	2	53	—	—	—	—	—	—	—	—
D. thea	—	1	3	—	—	—	—	—	—	—	—
Tritaeta gibbosa	—	—	1	—	—	—	—	—	—	—	1
Guernea coalita	—	—	6	—	3	7	—	9	—	—	—
Talitridae:											
Hyale prevosti	1	—	—	—	—	—	—	—	—	—	—
Aoridae:											
Aora typica	39	—	13	—	—	1	30	1	—	—	—
Lembos websteri	22	3	2	—	—	—	—	—	—	—	—
L. longipes	—	—	—	—	17	4	—	—	16	—	—
Photidae:											
Microprotopus maculatus	70	60	21	—	—	—	—	—	—	—	—
Photis longicaudata	—	—	—	—	—	8	2	11	—	—	—
Eurystheus melanops	—	—	1	—	—	—	—	7	—	—	—
E. erythrophthalmus	14	2	3	—	—	15	85	15	1	—	—
E. palmatus	—	—	—	—	—	1	6	8	3	—	—
Podoceropsis nitida	—	—	—	—	—	1	15	—	—	—	—
Megamphopus cornutus	1	—	22	4	—	27	3	41	1	—	—
Leptocheirus hirsutimanus	—	—	—	—	—	1	—	1	—	—	—
L. pectinatus	1	—	109	79	—	3	—	19	2	—	—
Amphithoidae:											
Amphithoë rubricata	—	—	2	—	—	—	—	—	—	—	—
Pleonexes gammaroides	—	—	1	—	—	—	—	—	—	—	—
Sunamphithoë pelagica	—	1	—	—	—	—	—	—	—	—	—
Jassidae:											
Jassa falcata	4	5	8	—	—	—	—	—	—	—	—
J. pusilla	—	—	—	—	—	1	3	6	—	—	—
Microjassa cumbrensis	1	—	7	—	—	13	8	21	—	—	—
Corophiidae:											
Ericthonius brasiliensis	15	—	15	—	—	—	13	1	—	—	—
Unciola planipes	—	—	—	—	2	—	—	—	—	—	—
Siphonoecetes dellavallei	4	63	35	—	—	—	—	—	—	—	—
Corophium affine	—	—	—	—	—	—	—	—	53	1	—
C. bonelli	2	—	—	—	—	—	—	2	—	—	—
Podoceridae:											
Dulichia porrecta	—	—	—	—	—	—	—	1	—	—	—
Caprellidae:											
Phtisica marina	28	4	114	3	—	10	69	11	16	—	—
Pseudoprotella phasma	40	—	12	—	—	—	2	—	—	—	—
Podalirius typicus	1	35	9	—	—	—	—	1	—	—	—
Parvipalpus capillaceus	—	—	—	—	—	—	—	1	—	—	—
Caprella acanthifera	41	9	9	2	—	—	—	1	—	—	—
C. linearis	2	2	—	—	—	—	61	—	—	—	—
C. fretensis	2	—	—	—	—	—	—	—	—	—	—

The number of species obtained is often great, and in haul no. 70, taken with a tow-net attached to the otter trawl, there were over 325 individuals belonging to thirty-three separate species; while on several occasions a haul of the small fine-meshed dredge, which was towed only a few yards, brought up over 100 individuals belonging to more than twenty species. As a rule two or three species are predominant and make up the greater part of the catch, but the majority are widely distributed on the kind of bottom that they favour. I have found the Amphipoda to be a dominant group, in numbers if not in bulk, on all types of offshore ground that I have investigated. It is therefore possible that they are of even greater economic importance than has been realized. They have been shown to be an important source of food for fish, especially young fish, and they are probably largely eaten by other animals upon which fish feed (see Hunt, 1925, and Steven, 1930).

Habitats of Offshore Species

I have compiled lists of the species which I consider to be significant for various habitats. These lists are obtained by finding the average number of individuals per haul of each species on the different grounds. They are not of equal value for each habitat, as the number of hauls taken varied from only three on a mud bottom to seventeen on a bottom of muddy sand with broken shell. The hauls also varied in distance covered and were taken with a variety of gear. The lists do not, therefore, provide any information as to the absolute density of population but they are an attempt at classification into habitat groups with an observed numerical basis, however imperfect.

In assessing the significance of any species on a particular ground I have included it where it has an average value per haul of 0·8 or more. This is an arbitrary figure which may be considered low, but the area covered by any one haul is usually small and when the species may be present in an average of eight hauls out of ten the total population on the ground is probably large. The average occurrence in hauls is not necessarily related to the average number of individuals per haul as the latter is sometimes brought up by large numbers in one or two hauls only, but on the whole the spreadover is fairly even and I have not thought it practical to discriminate between these two values. Habitat (1) consisted of weed, often lying loose on the bottom, mainly brought up in the otter trawl. Habitat (2) was to some extent mixed, as a certain amount of loose weed was present. Habitat (3) included parts of (1), (2) and (4). Habitat (7) consisted of hydroids and polyzoans usually attached to shells and stones on mixed grounds. Where the habitat is a combination of two or more of the others listed, that to which each species should properly be referred is indicated by the number set in heavier type following the name of the species. After the name of the species are also indicated (in brackets) the other habitats for which it was significant.

Species which are probably significant for Various Habitats

(1) Weed, including loose weed, on fine sand. Depth 4–22 m.

Apherusa bispinosa
Nototropis swammerdami
Dexamine spinosa
Aora typica (7)
Lembos websteri
Microprotopus maculatus (2)
Eurystheus erythrophthalmus (6, 7, 8)
Ericthonius brasiliensis (7)
Phtisica marina (6, 7, 9)
Pseudoprotella phasma
Caprella acanthifera

(2) Fine sand (with some loose weed). Depth 2–12 m.

Socarnes erythrophthalmus (4)
Bathyporeia guilliamsoniana
B. elegans
Urothoë elegans (9)
Stenothoë marina (1, 7)
Perioculodes longimanus (9, 10)
Pontocrates arenarius
Pontocrates norvegicus
Synchelidium haplocheles (6, 8)
Apherusa bispinosa (1)
Megaluropus agilis
Microprotopus maculatus (1)
Siphonoecetes dellavallei
Podalirius typicus

(3) Sand and fine gravel (with some weed). Depth 11–18 m.

Socarnes erythrophthalmus (2, 4)
Bathyporeia elegans (2)
Urothoë elegans (2)
Metaphoxus fultoni (4)
Gitana sarsi (4)
Lilljeborgia kinahani (4)
Perioculodes longimanus (2)
Pontocrates norvegicus (2)
Synchelidium haplocheles (2)
Apherusa bispinosa (1)
Nototropis vedlomensis (4)
Cheirocratus sundevalli (6)
Megaluropus agilis (2)
Ceradocus semiserratus (4)
Maera othonis (6, 7, 8)
Dexamine spinosa (1)
Aora typica (1)
Microprotopus maculatus (1)
Megamphopus cornutus (4)
Leptocheirus pectinatus (4)
Ericthonius brasiliensis (1)
Siphonoecetes dellavallei (2)
Phtisica marina (1)
Pseudoprotella phasma (1)
Podalirius typicus (2)
Caprella acanthifera (1)

(4) Stony gravel. Depth 18–35 m.

Socarnes erythrophthalmus (2)
Metaphoxus fultoni (6)
Gitana sarsi (8)
Lilljeborgia kinahani (6, 7)
Nototropis vedlomensis (6, 8)
Ceradocus semiserratus (6)
Megamphopus cornutus (6, 8)
Leptocheirus pectinatus (8)

(5) Coarse sand. Depth 18–35 m.

Bathyporeia gracilis
Maerella tenuimana
Guernea coalita
Lembos longipes (9)

(6) Coarse sand with broken shell. Depth 18–55 m.

Lysianassa plumosa (8)
Orchomenella nana
Urothoë marina
Metaphoxus fultoni (4)
Amphilochus manudens (7, 8)
Peltocoxa brevirostris (8)
Metopa bruzelii
Cressa dubia (7, 8)
Lilljeborgia kinahani (4, 7)
Synchelidium haplocheles (2, 8)

Stenopleustes nodifer
Nototropis vedlomensis (4, 8)
Melphidippella macra (8)
Eusirus longipes
Cheirocratus sundevalli (3)
Maera othonis (3, 7, 8)
Eurystheus erythrophthalmus (1, 7)
Megamphopus cornutus (4, 8)
Microjassa cumbrensis (8)
Phtisica marina (1, 7, 8)

(7) Hydroids and polyzoans, mainly on mixed grounds. Depth 20–82 m.

Amphilochus manudens (6, 8)
Stenothoë marina
S. antennulariae
Cressa dubia (6, 8)
Panoploea minuta
Lilljeborgia kinahani (4, 6)
Parapleustes monocuspis
Maera othonis (3, 6, 8)
Aora typica (1)
Eurystheus erythrophthalmus (1, 6)
Ericthonius brasiliensis (1)
Phtisica marina (1, 6, 8)
Caprella linearis

(8) Muddy sand with broken shell. Depth 27–38 m.

Lysianassa plumosa (6)
Ampelisca spinipes (9)
A. diadema (9)
A. tenuicornis (9)
Amphilochus manudens (6, 7)
Peltocoxa brevirostris (6)
Gitana sarsi (4)
Cressa dubia (6, 7)
Synchelidium haplocheles (2, 6)
Nototropis vedlomensis (4, 6)
Melphidippella macra (6)
Maera othonis (3, 6, 7)
Eurystheus erythrophthalmus (1, 6, 7)
Megamphopus cornutus (4, 6)
Leptocheirus pectinatus (4)
Microjassa cumbrensis (6)

(9) Muddy sand. Depth 31–82 m.

Scopelocheirus crenatus
Ampelisca spinipes (8)
A. diadema (8)
A. tenuicornis (8)
Urothoë elegans (2)
Harpinia pectinata
Harpinia crenulata (10)
Perioculodes longimanus (2, 9)
Lembos longipes (6)
Corophium affine
Phtisica marina (1, 6, 8)

(10) Mud. Depth 82–88 m.

Harpinia crenulata (9)
Metopa borealis
Perioculodes longimanus (2, 9)
Westwoodilla caecula

(11) Sponges, growing on a bed of *Modiolus*. Depth 60 m.

Perrierella audouiniana
Leucothoë spinicarpa
Colomastix pusilla
Tritaeta gibbosa

(12) Specialized habitats

Laphystius sturionis, parasitic on fish
Melita obtusata, on *Asterias* and *Luidia*
Podoceropsis nitida, in hermit crab shells
Jassa pusilla, in sponges on *Inachus*
Chelura terebrans, in submerged wood

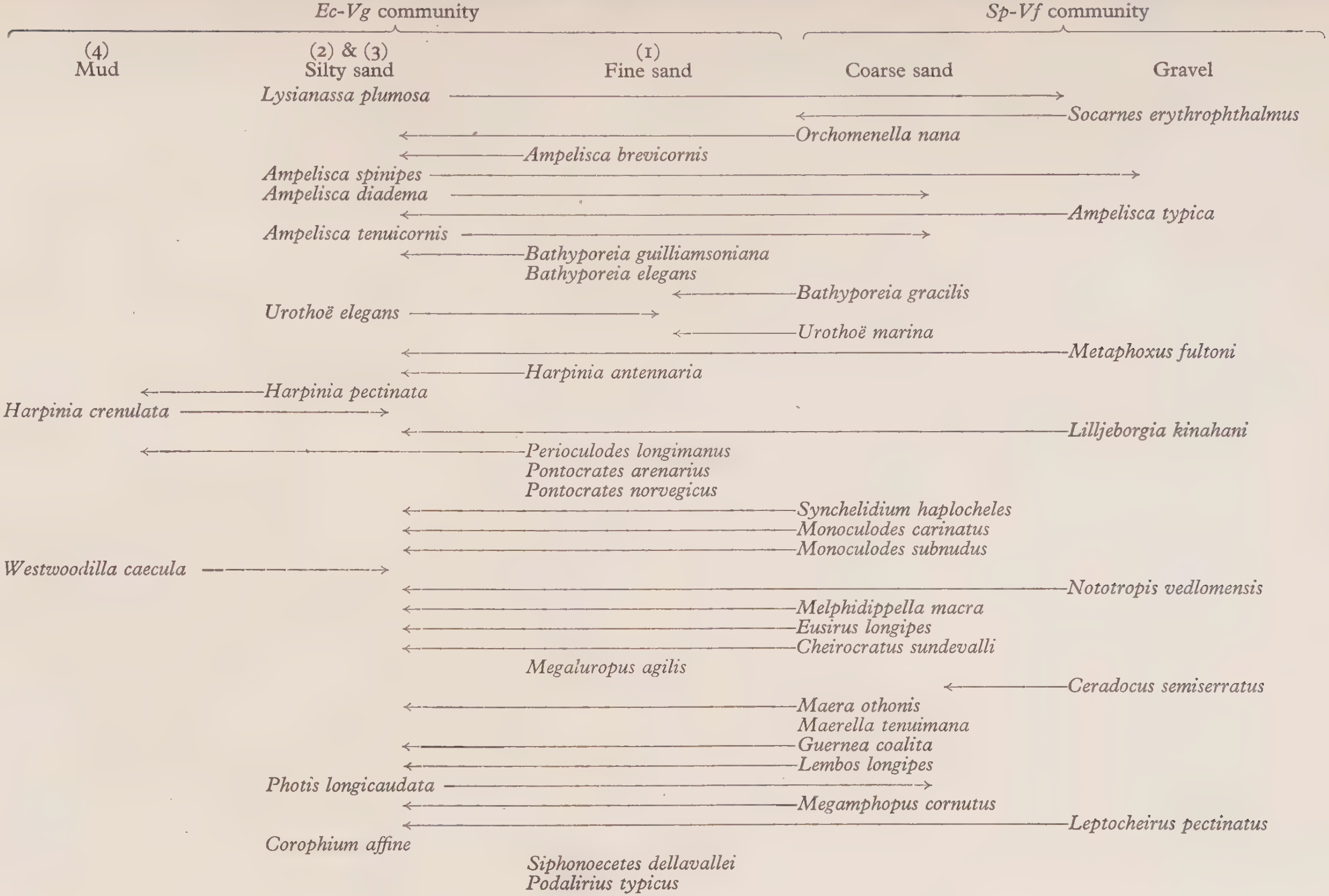
The habitats shown include all those that have been found offshore in the area. It will be seen that many species are common to two or more habitats or grounds, while some are confined to one, but where a species occurs on several grounds these have as a rule some common feature. Thus stony gravel and mixed grounds may be grouped together as containing coarse deposits. Some species which occur on algae also occur on hydroids. On the whole, in fact, the Amphipoda are quite selective with regard to the type of ground on which they live.

Certain closely related species occupy very different habitats in the same area. *Leucothoë spinicarpa* is associated, probably as a commensal, with sponges and ascidians, while *L. lilljeborgi* burrows in silty ground; *Nototropis swammerdami* lives on sublittoral algae while *N. vedlomensis* is found in mixed grounds and gravels; *Lembos websteri* occurs on algae mainly at low water while *L. longipes* probably burrows in various grades of sand in at least some metres depth. Differences in habitat of this description are not always so clear but in other genera a trend from one grade of deposit to another can be seen over a series of species as in the example of *Ampelisca* and *Harpinia* set out below. A similar trend may be observed among the closely related genera of the Oedicerotidae.

From the information so far obtained as to the distribution of the Amphipoda on various grounds some idea may be gained of the place of a number of species in the general schema of animal communities in the sea. In this matter I shall refer to the system used by Ford (1923). He divided the infaunal communities on the sea-bottom near Plymouth into two main series, the *Echinocardium cordatum-Venus gallina* (*Ec-Vg*) community characteristic of finer soils, and the *Spatangus purpureus-Venus fasciata* (*Sp-Vf*) community characteristic of coarser grades. The *Ec-Vg* series was divided into four subgroups, (1) being characteristic of clean sand, (2) and (3) of silty sand, and (4) of black mud. The communities in the neighbourhood of Port Erin fall within the limits of this system.

In the table below (Table II) certain species of Amphipoda from the area are referred to this system. As there is no rigid boundary between one community and another it is usually only possible to indicate a preference for one grade of deposit. An arrow-head opposite a specific name shows a tendency for that species to be found in mixed communities corresponding to a mixture of coarse and fine grades of deposit, or to occur in more than one grade. No species by itself could be used to diagnose the community in which it occurred, but a number of species together would provide a fairly sound indication of the other animals to be expected on the same ground.

TABLE II. HABITAT DISTRIBUTION OF OFFSHORE AMPHIPODA



Habitats of Intertidal Species

The intertidal forms, omitting estuarine and brackish-water species, may be grouped into two major divisions inhabiting rocky and sandy shores respectively, though a number of species are common to both. In each division most of the forms are more or less confined to definite zones in relation to tidal level.

The following include the more important species occurring in the area. Reference to tidal level is approximate.

(1) Rocky shores. Living under stones or among algae and in pools

Tidal zone	Species
H.W.S. and above	*Orchestia gammarella*
H.W.N.	*Marinogammarus marinus, Orchestia mediterranea, Hyale prevosti*
M.T.L.	*Marinogammarus marinus, M. obtusatus, M. finmarchicus, Hyale prevosti*
L.W.N	*Stenothoë monoculoides, Apherusa jurinei, Melita palmata, Marinogammarus obtusatus, M. finmarchicus, Hyale prevosti, Amphithoë rubricata*
L.W.S.	*Stenothoë monoculoides, Apherusa jurinei, Gammarellus homari, Tritaeta gibbosa, Aora typica, Lembos websteri, Eurystheus erythrophthalmus, Amphithoë rubricata, Jassa falcata, J. ocia, Parajassa pelagica, Corophium bonelli, Caprella acanthifera*

(2) Sandy shores

(*a*) Fine sand. All burrowing species

Tidal zone	Species
H.W.S.	*Talitrus saltator, Talorchestia deshayesei*
H.W.N.	*Haustorius arenarius*
M.T.L.	*Bathyporeia pelagica, Urothoë brevicornis, Pontocrates arenarius*
L.W.N.	*Bathyporeia pelagica, Urothoë brevicornis, Pontocrates arenarius, P. norvegicus*
L.W.S.	*Bathyporeia elegans, Urothoë brevicornis, Pontocrates arenarius, P. norvegicus*

(*b*) Muddy sand. Some burrowing species, but many found among algae at low water

Tidal zone	Species
H.W.S.	—
H.W.N.	*Corophium volutator*
M.T.L.	*C. volutator*
L.W.N.	*Melita palmata, Gammarus locusta*
L.W.S.	*Ampelisca brevicornis, Bathyporeia guilliamsoniana, Urothoë elegans, Harpinia antennaria, Perioculodes longimanus, Apherusa cirrus, A. bispinosa, Nototropis swammerdami, Melita hergensis, Gammarus locusta, Dexamine thea, Ericthonius brasiliensis, Corophium crassicorne*

The presence of muddy sand above low-water mark always indicates that the locality is sheltered from winds and currents and it is probably the shelter factor that favours the occurrence of most of the species in list (2*b*).

List (2*a*) was mainly compiled from collections made on the fine sand of Port Erin Bay. It may be compared with the data given for Kames Bay, Millport, by Watkin (1941), which may be set out as follows:

Tidal zone	Species
H.W.S.	—
H.W.N.	*Bathyporeia pilosa, Haustorius arenarius*
M.T.L.	*Bathyporeia pelagica, Urothoë brevicornis, Pontocrates norvegicus*
L.W.N.	*Bathyporeia pelagica, B. elegans, Urothoë brevicornis, Pontocrates arenarius, P. norvegicus*
L.W.S.	*Bathyporeia guilliamsoniana, B. elegans, Urothoë brevicornis, Pontocrates arenarius, P. norvegicus*

As Watkin was not concerned with the Talitridae it is evident that on the whole the two beaches show a similar amphipod fauna and zonation. The most striking difference is that *Bathyporeia pilosa* is present abundantly at Kames Bay but is absent from Port Erin Bay. This may be due to the absence of suitable ground about H.W.N. at Port Erin. The species probably occurs on the sandy shores at the north end of the Isle of Man, since it has been recorded from Millport and from the west coast of Wales. The density of population is generally lower at Port Erin than at Millport.

Colman (1940) investigated the faunas of intertidal seaweeds including *Laminaria digitata* holdfasts. It is interesting to compare the results for Plymouth and the Isle of Man for the latter habitat.

AMPHIPODA FROM *LAMINARIA* HOLDFASTS

Plymouth	Isle of Man
Stenothoë monoculoides	*Stenothoë monoculoides*
Apherusa jurinei	*Apherusa jurinei*
Tritaeta gibbosa	*Tritaeta gibbosa*
Lembos websteri	*Lembos websteri*
Eurystheus erythrophthalmus	*Eurystheus erythrophthalmus*
Amphithoë rubricata	*Amphithoë rubricata*
Jassa falcata	*Jassa falcata*
Caprella acanthifera	*Caprella acanthifera*
Leucothoë incisa	*Nannonyx goësi*
Elasmopus rapax	*Orchomene humilis*
Microdeutopus damnoniensis	*Gitana sarsi*
M. chelifer	*Leucothoë spinicarpa*
Microjassa cumbrensis	*Lilljeborgia brevicornis*
Podocerus variegatus	*Apherusa bispinosa*
Caprella linearis	*Dexamine thea*
	Hyale prevosti
	Aora typica
	Pleonexes gammaroides
	Jassa ocia
	Parajassa pelagica
	Ericthonius brasiliensis
	Corophium bonelli

Allowing for the fact that the investigations at Port Erin were more extensive and that a number of species were collected once only the two lists are very similar. Eight out of fifteen species recorded at Plymouth occur in the same habitat at Port Erin, and of the remaining seven *Leucothoë incisa*, *Elasmopus rapax*, *Microdeutopus chelifer* and *Podocerus variegatus* have not been recorded from the Isle of Man. It is evident that this habitat is an important one, as the population of the holdfasts is often very large. According to Colman there may be as many as 175 amphipods per 100 g. of damp weed. I have several times obtained 300 or more individuals from six medium-sized holdfasts of a total weight of about 300 g.

Goodhart & Harrison (1940) gave a list of six amphipods found on the shore above L.W.S. at Oldany Harbour, Sutherland. These were *Ampelisca spinimana*, *Harpinia antennaria*, *Leucothoë spinicarpa*, *Coremapus versiculatus*, *Phtisica marina* and *Caprella acanthifera*. With two exceptions they had not been recorded elsewhere between tide-marks. It was suggested as a possible explanation of this distribution that these species occurred above low-water mark only on coasts washed by the North Atlantic Drift.

At Port Erin four of these species occur and they have all been found above low-water mark, *Caprella acanthifera* sometimes abundantly. *Ampelisca spinimana* and *Coremapus versiculatus* have not been recorded from the area. The water near the coasts of the Isle of Man is considerably less saline than unaltered Atlantic water. There is a gradual diminution in surface salinity from St George's Channel towards the Lancashire coast, indicating a drift from south to north through the Irish Sea. The mean value near Port Erin is 34·1 ‰ (Proudman, 1946). There is probably no current from the North Channel reaching the Isle of Man. In view of these facts I do not think that the hypothesis of Goodhart and Harrison can be maintained.

It is unlikely that temperature or the time of occurrence of spring tides are controlling factors, since spring tides occur during the hottest part of the day in the north of Scotland (Reid, 1935).

It is more likely that the intertidal distribution of some amphipods is regulated by the amount of shelter available. All the records of the four species mentioned above in the Isle of Man were from locations affording a good deal of shelter from heavy seas, and which consequently contained a large amount of silt, and it is probably this last factor that the amphipods find favourable. In this connexion it is interesting to note that in Port St Mary Outer Harbour, which is almost completely protected from wave action, the sand at L.W.S. is rather muddy and contains among other species *Urothoë elegans*, *Harpinia antennaria*, *Perioculodes longimanus* and *Podalirius typicus*, none of which is frequently found above low-water mark.

It is possible that the scarcity of intertidal records from other districts is merely due to the comparative lack of intensive collecting.

Brackish-Water and Estuarine Habitats

It will be convenient to describe three locations in the area in which the distribution of the amphipods is affected by variations in salinity.

Spaldrick

This location is situated at the north side of Port Erin Bay. It consists of a rocky beach with a small fresh-water stream emptying on to the beach over a fall just above H.W.S., and running into the sea through stones and boulders covered with *Fucus* and *Ascophyllum*. In the summer the stream is often reduced to a mere trickle. The animals living in the stream are therefore subjected to considerable variations in salinity, especially during spring tides, from almost fresh water at low tide when the stream is in flood to almost full salinity at high tide when the stream is low. In winter the salinity under the fall reaches about 17 ‰ at H.W.S. The whole tidal zone will be subjected to these extremes for varying periods, the inhabitants of the topmost zone living in fresh water for most of the time and those of the lowest zone in sea water except for short periods at L.W.S. The length of the beach from high- to low-water mark is about 70 yards.

Brewery Beach

This location is situated just east of Gansey. A fresh-water stream enters the shore through a tunnel just above H.W.S. and runs over rock with scattered stones to below H.W.N., the remainder of its course over the shore being over fine sand with a number of flat stones down to L.W.N. The amphipods occur under the stones. The stream is rather larger than that at Spaldrick. The distance from high- to low-water mark is about 120 yards. Fig. 1 shows the relative distributions of the amphipod species found in these two streams.

Salinity conditions are approximately the same at both locations.

It will be seen that the zonation of species common to both streams is generally similar. At Spaldrick the presence of *Marinogammarus obtusatus* and *M. finmarchicus* may be regarded as accidental since both species are much more abundant outside the limits of the stream. They are evidently able to tolerate almost fresh water for some hours at a time. *Hyale prevosti* and *Melita palmata* are also more abundant away from the stream at both locations. *Marinogammarus marinus* is abundant both in and away from the streams, but extends to a lower level on the shore where there is fresh-water influence. The remaining species are confined to the area of the streams. At both places the brackish-water type of *Gammarus duebeni* occurs from about H.W.S. to H.W.N. At Spaldrick this species also occurs for some distance up the stream to a height of at least about 100 ft. above sea-level. Since the stream enters the shore over a fall there is a distinct break in the distribution of *G. duebeni*, and presumably the animals found above the fall belong to the fresh-water type.

The species is apparently absent above the shore at Brewery Beach since a number of collections in the stream failed to produce any. I am unable to give any reason for its absence from the upper reaches.

Marinogammarus pirloti occupies much the same zone as *M. marinus* at Brewery Beach but is absent from Spaldrick, and *Gammarus zaddachi salinus* occurs from about M.T.L. to L.W.N. at Brewery Beach but not at Spaldrick. Since the salinity conditions are much the same in both streams some other factor must control their distribution and the most obvious one is the nature of the ground over which the streams flow. At Brewery Beach the stream flows over sand from just below H.W.N. to low-water mark, while at Spaldrick the whole course is over rocks and through boulders. It is possible that *Marinogammarus pirloti* and *Gammarus zaddachi* can establish themselves only where fine deposits are present.

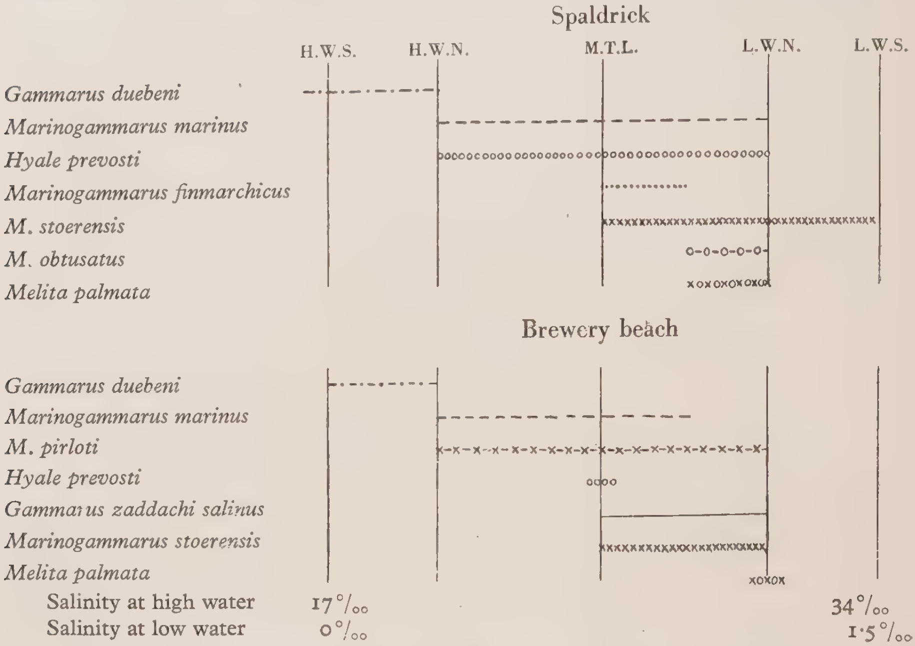


Fig. 1. The relative distributions of various amphipods in the streams at Spaldrick and Brewery Beach. The vertical lines indicate the tidal level. Limits for each species are only approximate.

The Silverburn

This is the only stream in the area of this survey with a distinct estuary. It is a small river which enters the sea through Castletown Harbour. At L.W.S. the whole of the estuary is emptied of sea water. The length of the tidal zone is about ½ mile but the upper 400 yards of this zone is tidal only when high tide at

Liverpool reaches 28 ft. or more above datum, that is during H.W.S. This effect is due to the stream passing over a weir above which neap tides do not reach. The amphipod fauna lives among algae and fresh-water vegetation and under stones on the bottom of the stream and on the banks. Those animals which live in the stream below the weir will be subjected to considerable salinity changes twice daily, the range depending on the distance from the harbour mouth. Individuals living on the banks above the stream will not experience the lower limits of the salinity range. Above the weir the animals will remain in fresh water for long periods but will at intervals experience a slight rise in salinity. The distribution of the amphipods in the Silverburn is indicated in Fig. 2.

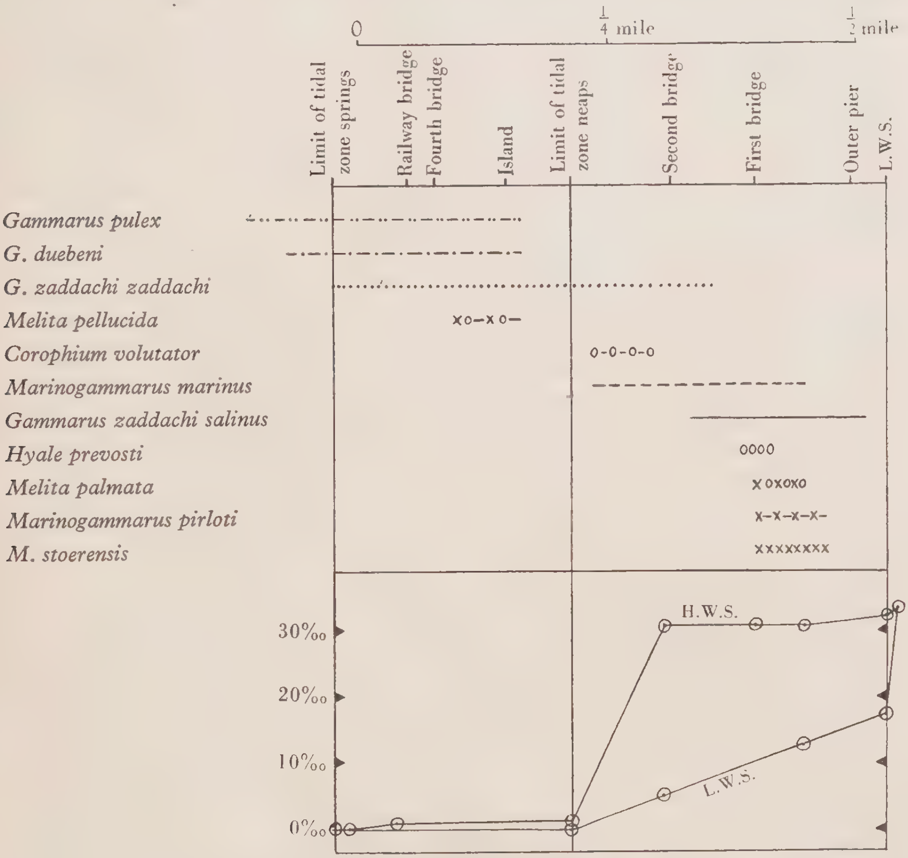


Fig. 2. The relative distribution of the amphipods in the Silverburn. The salinity diagram is based on samples taken near the bottom with a reversing water-bottle.

The species which inhabit that part of the estuary which is subjected to a wide range in salinity, i.e. the region below the upper limit of neap tides, occupy zones comparable to those which they inhabit on the shore. *Marinogammarus marinus*, *M. stoerensis*, *M. pirloti*, *Hyale prevosti* and *Melita palmata* are confined to this region. Their distribution may be compared with that shown in Fig. 1.

Gammarus zaddachi salinus is confined to the region in which the salinity at high water rises to 33 ‰ at the bottom, and in this respect experiences similar conditions to those on the shore at Spaldrick and Brewery Beach. *Gammarus zaddachi zaddachi* overlaps *G. z. salinus* for a short distance but extends upwards to the limits of the tidal zone where the salinity does not rise above 1 ‰.

Melita pellucida and *Gammarus duebeni* occupy the region of small salinity variation, the latter species extending a short distance into the region of permanently fresh water. Since its range corresponds with the lower part of that of *G. pulex* it is presumably the fresh-water type (Reid, 1939). The reason for its absence from the upper part of the river is unknown but it may be due to competition with *G. pulex*.

Comparison of the distribution of the amphipods in the Silverburn with those known in other estuaries, as indicated by Bassindale (1942) and revised by Spooner (1947), reveals no great anomalies.

The presence of *G. duebeni* and *G. pulex* in the same zone appears to be unusual, but in most of the estuaries previously investigated the fresh-water type of *G. duebeni* is probably missing.

G. locusta is often present near the mouths of estuaries. Its absence from the Silverburn is probably due to the steep salinity gradient at the mouth where the salinity falls below the normal lower limit for the species.

In other respects a reasonable agreement is shown with previous descriptions of estuarine zonation.

In any consideration of the distribution of *Gammarus* species in an estuarine or brackish-water habitat the possibility of the existence of local races must be taken into account. It is evident that the range of salinities in which the various species of this genus occur cannot be strictly defined at present, though recent work has gone a long way towards elucidation of this problem. The species which are most difficult to fit into any classification of habitats are *G. duebeni*, *G. zaddachi* and *G. locusta*. There appear to be two types of *G. duebeni* adapted respectively to brackish and fresh water, but they cannot be separated by any morphological criterion (Reid, 1939). *G. zaddachi*, on the other hand, may be grouped according to external characters into three subspecies (Spooner, 1947, and Segerstråle, 1947). *G. locusta* is a marine species and is usually intolerant of salinities below about 28 ‰ but in some locations, as in the Baltic (Segerstråle, 1946), it lives in greatly reduced salinities.

It seems probable that the genus *Gammarus* is in a state of active evolution. There is evidently more than one form of each of the three species mentioned and even where no alteration in external characters has taken place there appear to be physiological races. Huxley (1942, p. 279) suggested that the explanation of the occurrence of *G. duebeni* in the fresh waters of Ireland lies in its adoption of a peculiar habitat in atypical conditions at the margin of its range, an occurrence that has been observed in other animals. Salinity is the most obvious factor controlling the evolution of races in the genus and it is not unlikely that in regions of very gradual salinity change forms have evolved which are adapted to different conditions from those in which the parent species is found. These forms may then be able to colonize new areas and, in the absence of interspecific competition, to establish themselves. The presence of *G. duebeni* in the fresh waters of Ireland and its virtual absence from those of England may be due to the fact that *G. pulex* is a more successful competitor but has never become established in Ireland.

The manner in which an amphipod adapted to brackish water extends its range is unknown. There is no possibility of transport of the eggs since they are always carried by the female until hatched. Some species can tolerate high salinities for long periods and can even be bred in sea water in the laboratory (Sexton, 1928), and it is possible that they may occasionally be carried from one estuary to another by way of the sea; however, there are few authentic records of the capture of brackish-water species under fully marine conditions. The most probable method of transport from one brackish-water situation to another is on the bodies of birds as suggested by Segerstråle (1946).

SUMMARY

A survey was made during 1946 covering the Amphipoda of the south end of the Isle of Man from an ecological aspect. The object was to revise the records of the area and to obtain additional information about the habitats of the species found.

The area in which the survey took place was within a radius of 10 miles from Port Erin.

Various sorts of gear were used for collection offshore and it is concluded that the fine-meshed dredge is the most useful instrument for collecting amphipods.

A systematic treatment of the species found includes a summary of records regarding habitat for each species.

It is suggested that the Amphipoda may be of greater economic importance than has previously been realized.

A discussion of offshore, intertidal, and brackish-water habitats includes lists of the more important species obtained grouped according to type of ground and zonation with regard to tidal level and salinity. The importance of offshore species is assessed on a basis of the average number of individuals collected per haul.

Comparison of the zonation of littoral and estuarine species with that known from other areas reveals a general agreement.

The existence of more than one form of several species of the genus *Gammarus* is discussed and it is suggested that they are in an active state of evolution.

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APPENDIX I

Additions to the Fauna of the Isle of Man

The following species are here recorded for the first time from the area:

Acidostoma obesum (Bate)
Nannonyx spinimanus Walker
Tryphosa sarsi Bonnier
Tryphosites longipes (Bate & Westwood)
Ampelisca diadema (Costa)
Bathyporeia gracilis G. O. Sars
Urothoë elegans Bate
Harpinia pectinata G. O. Sars
Amphilochus spence-batei Stebbing
Metopa borealis G. O. Sars
M. pusilla G. O. Sars
Laphystius sturionis Kröyer
Monoculodes subnudus Norman
Calliopius crenulatus Chevreux & Fage
Parapleustes monocuspis (G. O. Sars)
Epimeria cornigera (J. C. Fabricius)
Cheirocratus intermedius G. O. Sars
Melita hergensis Reid
Gammarus pulex (L.)
Marinogammarus finmarchicus (Dahl)
M. stoerensis (Reid)
Pectenogammarus planicrurus Reid
Microdeutopus damnoniensis Bate
Eurystheus melanops (G. O. Sars)
Protomedeia fasciata Kröyer
Isaea montagui Milne-Edwards
Sunamphithoë pelagica (Milne-Edwards)
Biancolina cuniculus Stebbing
Unciola planipes Norman
Corophium crassicorne Bruzelius
C. affine Bruzelius
Parvipalpus capillaceus (Chevreux)
Caprella acutifrons Latreille
C. fretensis Stebbing
Themisto abyssorum (Boeck)

APPENDIX II

OTHER RECORDS AND CORRECTIONS

The following species have been recorded from the area previously but were not collected during the course of this survey:

Normanion quadrimanus (Bate & Westwood)
Harpinia laevis G. O. Sars
Peltocoxa marioni Catta
Parapleustes assimilis (G. O. Sars)
Calliopius laeviusculus Kröyer
Ericthonius difformis Milne-Edwards
Siphonoecetes colleti Boeck

The following species have been recorded incorrectly from the area (Marine Fauna of the Isle of Man, 1937, and additions in *Annual Reports*, Marine Biological Station, Port Erin):

Amphilochoides odontonyx Boeck. Walker's original record was named in accordance with Sars (1895), and should have been referred to *A. serratipes* (Norman).

Apherusa ovalipes Norman & Scott. Examination of the specimens in the collection referred to this species shows that they are all *A. bispinosa* (Bate).

Gammarus campylops Leach. These were probably immature specimens of *G. locusta* and possibly of *G. zaddachi*. *G. campylops* is now a doubtful species (Sexton & Spooner, 1940).

Leptocheirus pilosus Zaddach. Walker's original record refers to *L. pectinatus* Norman.

Jassa dentex (Czerniavski). The forms referred to this species should now be included under *J. falcata* (Montagu).

APPENDIX III

RECORD OF HAULS TAKEN OFFSHORE

Serial no.	Date	Position	Type of bottom or contents of haul	No. of species	No. of individuals	Depth (m.)	Gear used
1	29. iii. 46	¾ mile W. of Bradda Head	Coarse sand	1	1	27	Naturalist's dredge
2	8. iv. 46	¾ mile N. of Kitterland	Algae on sand and broken shell	6	13	22	N.D.
4	10. iv. 46	½ mile N. of Fleshwick	Stony gravel	7	119	15	Small fine-meshed dredge
5	12. iv. 46	1 mile N. of Kitterland	Coarse sand and broken shell	5	36	27	N.D.
6	12. iv. 46	Inside Port Erin Bay	Fine sand with algae	8	22	6–9	Small F.-M.D.
7	16. iv. 46	¾ mile N.W. of Bay Fine	Hydroids on broken shell	8	71	27	N.D.
8	17. iv. 46	1 mile N. of Kitterland	Coarse sand and broken shell	7	61	27	N.D.
9	24. iv. 46	Mouth of Port Erin Bay	Fine sand with algae	7	24	9–13	D-net
10	24. iv. 46	Inside Port Erin Bay	Fine sand with weed	12	36	4–9	D-net
11	25. iv. 46	½ mile W.S.W. of Bradda	Coarse sand and broken shell	7	14	29	N.D.
12	26. iv. 46	1 mile W.N.W. of Bradda	Muddy sand and broken shell	6	9	29	D-net
13	26. iv. 46	Inside Port Erin Bay	Algae on sand	10	34	4–9	D-net
14	1. v. 46	1½ miles W.N.W. of Bradda	Muddy sand and broken shell	8	14	33	N.D.
16	3. v. 46	3 miles W.N.W. of Charran	Muddy sand and broken shell	6	21	33	Small F.-M.D.
17	3. v. 46	Mouth of Port Erin Bay	Fine sand with algae	10	27	9–13	D-net
18	8. v. 46	2 miles W.N.W. of Charran	Muddy sand and broken shell	18	46	31	Small F.-M.D.
19	10. v. 46	½ mile N.W. of Fleshwick	Fine sand with weed	5	5	11–15	Small F.-M.D.
20	10. v. 46	Off Raglan Pier, Port Erin Bay	Fine sand with weed	12	158	2–4	Small F.-M.D.
21	13. v. 46	50 yards off Bay Fine	Sand and stony gravel	15	170	11–15	Small F.-M.D.
22	13. v. 46	N. side of Port Erin Bay	Fine gravel and sand	14	68	18–11	Small F.-M.D.
23	15. v. 46	2 miles W.N.W. of Bradda	Muddy sand and broken shell	15	40	33	Small F.-M.D.

24	17. v. 46	50 yards off Bradda	Stony gravel	4	7	22–27	Small F.-M.D.
26	20. v. 46	N. side of Port Erin Bay	Fine gravel and sand	29	114	7–15	Small F.-M.D.
27	20. v. 46	Inside Port Erin Breakwater	Fine sand with weed	28	156	11	Small F.-M.D.
28	24. v. 46	6 miles W.N.W. of Fleshwick	Muddy sand	6	20	46	Small F.-M.D.
29	14. vi. 46	400 yards off Bay Fine	Sand and fine stony gravel	15	22	18	Small F.-M.D.
30	14. vi. 46	Off Raglan Pier	Fine sand with weed	5	162	2–4	Small F.-M.D.
31	15. vi. 46	Bay Fine to Port Erin Breakwater	Algae on sand and gravel	5	6	18–11	Otter trawl
32	19. vi. 46	¾ mile W.N.W. of Bradda	Muddy sand and broken shell	25	81	29	Small F.-M.D.
33	19. vi. 46	N. side of Port Erin Bay	Sand and fine gravel	18	76	15–18	Small F.-M.D.
34	21. vi. 46	2½ miles W. of Bradda	Muddy sand and broken shell	24	46	33	Small F.-M.D.
35	21. vi. 46	1½ miles W. by N. of Bradda	Muddy sand and broken shell	9	15	31	Small F.-M.D.
36	24. vi. 46	2 miles N.W. of Kitterland	Coarse sand and broken shell	18	60	31	Small F.-M.D.
37	24. vi. 46	2½ miles N. by W. of Kitterland	Muddy sand and broken shell	10	24	33	Small F.-M.D.
38	26. vi. 46	2½ miles W.N.W. of Kitterland	Muddy sand and broken shell	9	12	31	Small F.-M.D.
39	26. vi. 46	2 miles W.N.W. of Charran	Muddy sand and broken shell	13	30	33	Small F.-M.D.
40	1. vii. 46	½ mile N.N.W. of Calf Stack	Coarse sand and broken shell	20	128	33	Small F.-M.D.
41	1. vii. 46	Bay Fine to Breakwater	Algae on sand and gravel	5	15	18–11	Otter trawl
42	3. vii. 46	3½ miles W. of Bradda	Coarse sand	6	33	35	Small F.-M.D.
43	8. vii. 46	3 miles N. by W. of Calf Stack	Hydroids on coarse sand and shells	6	10	33	Small F.-M.D.
44	8. vii. 46	2 miles W. by S. of Bradda	Coarse sand and broken shell	8	11	31	Small F.-M.D.
45	10. vii. 46	Bradda Head to Breakwater	Algae on fine sand	6	42	18–11	Otter trawl
46	11. vii. 46	Bay Fine to Breakwater	Algae on sand and gravel	8	29	18–11	Otter trawl
48	12. vii. 46	½ mile N. of Fleshwick	Fine stony gravel	14	132	11–15	Small F.-M.D.

APPENDIX III (*cont.*)

Serial no.	Date	Position	Type of bottom or contents of haul	No. of species	No. of individuals	Depth (m.)	Gear used
49	16. vii. 46	½ mile N. of Bay Fine	Sand and fine gravel	7	18	15–18	Small F.-M.D.
50	16. vii. 46	Mouth of Port Erin Bay	Fine sand with weed	10	22	11–15	Small F.-M.D.
51	24. vii. 46	2 miles S. of Kitterland	Hydroids on shell gravel	6	116	18–22	Otter trawl
53	26. vii. 46	¾ mile W. of Bradda	*Nemertesia* on shell	4	8	29	On long line
54	1. viii. 46	5 miles N.W. by W. of Bradda	Muddy sand	13	46	59	Large F.-M.D.
55	1. viii. 46	5 miles N.W. by W. of Bradda	Hydroids on muddy sand	7	56	55	Scallop dredge
56	8. viii. 46	6 miles W. of Port Erin	Muddy sand	14	30	61	Large F.-M.D.
57	8. viii. 46	6 miles W. of Port Erin	Hydroids on muddy sand	9	38	64	S.D.
58	16. viii. 46	1½ miles W.N.W. of Bradda	Muddy sand and broken shell	18	28	31	Large F.-M.D.
59	16. viii. 46	Bradda Head to Breakwater	Algae on sand	13	32	18–11	Otter trawl
60	16. viii. 46	Bay Fine to Breakwater	Algae on sand and gravel	12	71	18–11	Otter trawl
61	20. viii. 46	3 miles S.E. of Kitterland	Hydroids on stones	14	123	37	S.D.
62	20. viii. 46	3 miles S.E. of Kitterland	Hydroids on stones and gravel	9	26	37	Large F.-M.D.
63	21. viii. 46	2½ miles W. of Port Erin	Coarse sand and broken shell	11	21	33	Large F.-M.D.
64	26. viii. 46	8 miles W.N.W. of Port Erin	Mud	5	11	82	Young fish trawl
65	26. viii. 46	8 miles W. ½ N. of Bradda	Muddy sand	10	24	82	Large F.-M.D.
66	26. viii. 46	8 miles W. by N. of Bradda	Hydroids on muddy sand	11	46	82	Otter trawl
67	2. ix. 46	5 miles S. of Spanish Head	Sponges on *Modiolus*	4	20	60	N.D.
68	2. ix. 46	5 miles S. of Spanish Head	Hydroids on *Modiolus*	13	61	60	N.D.
69	4. ix. 46	Bay Fine to Breakwater	Sand and fine stony gravel	19	108	18–11	Bottom tow-net
70	11. ix. 46	Bay Fine to Breakwater	Sand and gravel	33	325	15–11	Bottom tow-net
71	20. ix. 46	Mouth of Port Erin Bay	Fine sand with weed	14	85	7–15	Bottom tow-net
72	20. ix. 46	Mouth of Port Erin Bay	Algae on sand	16	214	7–15	Otter trawl
73	24. ix. 46	1 mile N. of Bay Fine	Coarse sand and broken shell	20	57	26	Large F.-M.D.
74	25. ix. 46	400 yards off Bay Fine	Sand and fine gravel	25	178	18	Large F.-M.D.

75	30. ix. 46	4½ miles S.W. by W. of Calf Stack	Coarse sand and broken shell	13	48	55	Large F.-M.D.
76	1. x. 46	1½ miles W. of Charran	Muddy sand	8	25	31	Large F.-M.D.
77	3. x. 46	8½ miles N.W. by N. of Bradda	Mud	3	8	88	Large F.-M.D.
78	7. x. 46	3 miles W.N.W. of Dalby	Muddy sand and broken shell	10	30	38	Large F.-M.D.
79	7. x. 46	½ mile W. of Cronk-ny-Arrey-Laa	Fine stony gravel	9	23	18	Large F.-M.D.
80	10. x. 46	50 yards off S.W. of Calf	Coarse sand	2	2	18	Large F.-M.D.
81	10. x. 46	1½ miles N. of Calf Stack	Hydroids on sand and shells	24	192	33	N.D.
82	14. x. 46	2½ miles W.N.W. of Charran	Muddy sand and broken shell	15	29	33	Large F.-M.D.
83	22. x. 46	400 yards N. of Bay Fine	Submerged wood	4	108	18	Otter trawl
84	23. x. 46	½ mile W. of Bradda	Muddy sand and broken shell	25	97	27	Large F.-M.D.
85	29. x. 46	Breakwater to Castle Rock	Sand and fine gravel	27	536	11–15	Bottom tow-net
87	29. x. 46	Inside Port Erin Bay	Fine sand	10	204	2–4	Large F.-M.D.
88	15. xi. 46	½ mile N. of Bay Fine	Algae on sand and broken shell	6	30	22	S.D.
89	16. xi. 46	Inside Port Erin Bay	On dead fish	1	50	4	Lobster pot
90	29. xi. 46	2½ miles W. by S. of Bradda	Coarse sand and broken shell	17	37	33	Large F.-M.D.
91	18. iv. 47	1½ miles N. of Kitterland	Coarse sand and broken shell	20	120	31	Large F.-M.D.
92	5. v. 47	2½ miles N.W. of Bradda	Muddy sand and broken shell	16	55	33	Large F.-M.D.
93	7. v. 47	2 miles W.N.W. of Bradda	Muddy sand and broken shell	14	46	33	Large F.-M.D.
94	9. v. 47	1 mile N.W. of Bay Fine	Coarse sand and broken shell	16	55	29	Large F.-M.D.
95	12. v. 47	Inside Port Erin Bay	Fine sand	6	48	8	Large F.-M.D.
96	12. v. 47	Off Castle Rock	Sand and fine gravel	12	78	8	Large F.-M.D.
97	13. v. 47	5½ miles N.W. by W. of Bradda	Muddy sand	8	101	59	Large F.-M.D.
98	16. x. 47	9 miles W.N.W. of Bradda	Mud	7	60	84	Young fish trawl

A NEW SPECIES OF CILIATE, *TRICHODINA BRANCHICOLA*, FROM SOME FISHES AT PLYMOUTH

By Yogendra R. Tripathi
(India State Scholar)

From the Plymouth Laboratory

(Text-figs. 1, 2)

While examining fishes at Plymouth for parasites I found the gills of eight species of Teleosts infected with a new urceolarid peritrich ciliate which I describe here as *Trichodina branchicola* n.sp. I also found the same species on rocklings (*Ciliata mustela* and *Gaidopsaurus tricirratus*) at Roscoff in March 1947.

All the fishes were caught at Plymouth and examined fresh, studies being made on living as well as fixed material. The living ciliates were stained with neutral red and methylene blue (1 : 5000 in sea water). The fixatives used were Bouin-Duboscq's fluid, Zenker's fluid (with formalin) and 2% aqueous osmium tetroxide. The slides were stained in iron-alum-haematoxylin with eosine, or in Delafield's haematoxylin with or without eosine.

The host species and the incidence of infection are shown in Table I.

TABLE I

Host species	No. examined	No. infected
Ciliata mustela (L.)	26	21
Gaidopsaurus tricirratus (Bloch)	8	6
Cottus bubalis Euphrasen	4	4
Spinachia spinachia (L.)	4	3
Blennius pholis L.	2	2
B. gattorugine Bloch	1	1
Trigla lucerna L.	1	1
Pleuronectes platessa L.	1	1

The intensity of infection was generally high in the first five and low in the last three hosts, but no exact quantitative studies of the parasitic population were made. *Ciliata mustela*, which is normally heavily parasitized, had a low grade of infection by *Trichodina branchicola* when caught from the brackish water of the Laira estuary near Plymouth. Four specimens of this fish taken from the estuary after a heavy rainfall had an appreciably low infection.

The following experiment supports the view that reduction in salinity of the water was the operative factor in reducing the parasitic population. The infected gills of *Ciliata mustela* were placed in diluted sea water (75 c.c. sea water and 25 c.c. distilled water) and it was found that after 3 hr. the ciliates were dead. The experiments were conducted in a bath of circulating sea water to ensure the requisite low temperature. Casual observations have repeatedly shown that *Trichodina branchicola* n.sp. is far more sensitive to changes of temperature and salinity than its hosts. This evidence tends to show that this species of *Trichodina* is a stenohaline organism and will not be found on fresh-water fishes.

After removal from its fish host *T. branchicola* does not survive in sea water for more than 2–3 hr.: it may live much longer on the dead host provided that it is kept at a low enough temperature. I have observed the ciliates still moving 32 hr. after the infected gills were removed from *Ciliata mustela* and had been placed in a refrigerator, although the sea water covering them had a thin film of ice. Richardson (1938) has done some experiments to show the viability of *Cyclochaeta domerguei* Wallengren, under different temperatures and salinity. Fresh-water fishes when infected with *Trichodina* spp. in the hatcheries are cured of the infection by a bath in saline water, or by putting them 'for 1 hour in a solution composed of 1 part of formalin (40%) to 4000 parts water' (Davis, 1947).

In *Ciliata mustela* and *Gaidopsaurus tricirratus* the only other gill parasite was a species of *Gyrodactylus*. This monogenean occurred as a moderate infection irrespective of the presence of *Trichodina branchicola* and there is no reason to think that they are incompatible.

In one *Spinachia spinachia* examined on 9 July 1946 the gills were infected with a species of *Amoeba* (6–11 μ in diameter) and hardly a dozen *Trichodina branchicola* were present. None was found to be infected by the *Amoeba*. The high infection of *Amoeba* was associated with hyper-secretion of mucus. *Trichodina branchicola*, normally a very actively moving animal, was hampered in its movements by the presence of the viscous mucus on the gills, and this may account for the unusually low infection. Chatton (1910) has described *Amoeba mucicola* infecting *Trichodina labrorum* Chatton 1910, from the gills of *Symphodus tinca*, but does not mention any pathological effect on the ciliate.

MORPHOLOGY

The shape of the organism is surprisingly variable. The oral or anterior end is strongly arched and the saucer shape of the posterior or aboral end is maintained by the 'skeletal complex', which in life is applied to the gill surface of the host (Figs. 1*b*; 2*a*, *b*). The general shape may be hemispherical or subspherical. When viewed from above the organism is round (30–53 μ in diameter) (Fig. 1*a*, *b*). Its height (antero-posterior) is 22–36 μ.

In the genus *Trichodina* there are two rings of cilia, an anterior oral and a posterior aboral ring—the latter is the chief organ of locomotion. In between these two rings of cilia is the velum—a fold of protoplasmic pellicle, capable of great extensions and contractions (Fig. 2*a*, *b*). It attains its greatest size when the animal is crawling on the gills or moving freely in the water (as seen on the slide under the microscope), and almost disappears when the animal is motionless or nearing death.

On the posterior surface, internal to the aboral ring of cilia, lies the 'skeletal complex' composed of the outer striated and the inner denticulate rings (Figs. 1*b*; 2*b*, *c*).

The skeletal complex and the centre of the ring are covered by a thin protoplasmic pellicle (Fig. 2*b*). The denticulate ring (10–19 μ in diameter) consists of 20–26 denticles. The following table shows the percentage of individuals with different numbers of denticles and the average diameter of the ring. These measurements are from 142 individuals from a single *Ciliata mustela*.

No. of denticles	...	20	21	22	23	24	25	26
Percentage of organisms	...	5	26·4	29·5	17·2	12·7	5	4·3
Average diameter of the ring (μ)	...	12·8	13	13·5	14·8	15·2	15·6	16

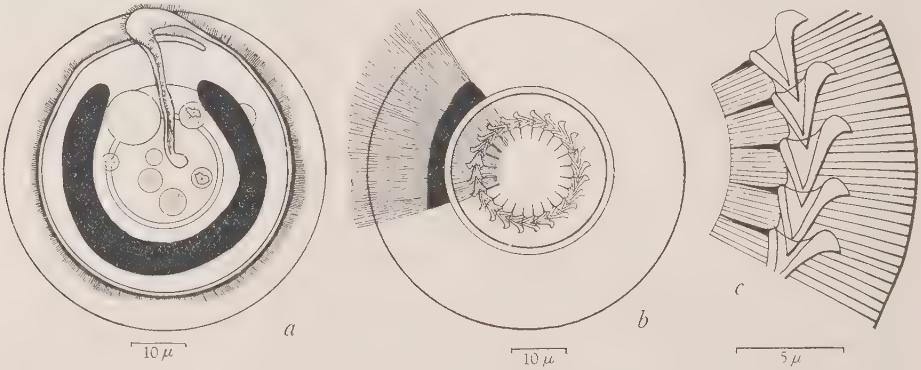

Fig. 1. *Trichodina branchicola*: *a*, anterior view showing oral groove and contractile vacuole and macronucleus; *b*, posterior view showing the skeletal complex and aboral cilia; *c*, portion of skeletal complex (further magnified).

The highest percentage of individuals is with 22 denticles; individuals with 21 and 23 denticles coming second and third. The size of the ring increases with the number of the denticles. Each denticle (Fig. 1*c*) is cone-shaped, 1·5–2·0 μ thick and 3·5 μ long, with a broad curved hook (2·3 μ long) on the outer side. The concave side of the hook is slightly thicker than the convex side. Each hook is attached to the cone at an angle like an oar. On the inner side of the cone there is a ray (3·2 μ long) pointing centrally and slightly anteriorly. It is thicker at the base, tapering towards the centre. In young *Trichodina branchicola* which has just undergone fission the number of denticles is halved, being 10–13 only. The outer hook is a little in front of the inner ray, as in *T. truttae* Mueller, and not exactly opposite, as in *T. pediculus* Ehrb. as described by Mueller (1937). The denticulate ring stains beautifully red with eosine and this helps very much in counting the number of denticles under the oil immersion lens.

External and somewhat anterior to the denticulate ring is a striated ring band 19–33 μ in diameter (Figs. 1*b*, *c*; 2*c*). There are six striae to each denticle. Each stria extends inwards as far as the inner ray. Each also is connected with the ciliary girdle by a strand of material which takes up the eosine stain less readily than the stria. Mueller (1938) supposed these structures to be myonemes. The outer borders of the striae fuse to form the edges of the adhesive disk. Each stria is thicker at the outer ends and tapers towards the centre. The ciliate secures itself to the gill surface with the adhesive disk. The skeletal complex is capable of movement as a whole in the horizontal plane but whether it can move in the antero-posterior direction as well is not clear.

The aboral cilia, 15–20 μ long, are fused at their base to form a thin membranelle, their distal ends being free (Figs. 1*b*; 2*c*). In *T. pediculus* Ehrb., *T. steinii* (Clar. & Lach.) and *T. renicola* (Mueller) the cilia are fused to form a series of membranelles. In the present species there is one continuous membranelle like that in *T. spheroidesi* Padnos & Nigrelli. The cilia do not fuse to form any membranelle in *T. halli* Padnos & Nigrelli and *T. urinicola* Fulton.

The oral groove runs round the anterior surface of the organism and makes little more than one anti-clockwise turn and then descends into the vestibulum which is connected with the gullet at its posterior end (Figs. 1*a*; 2*b*). The vestibulum descends obliquely and makes an angle of nearly 45° with the vertical axis of the organism. The base of the groove is slightly thickened and from its edges two parallel rows of cilia arise which are fused at their bases to form two parallel membranelles. The outer cilia are slightly longer than the inner. The inner membranelle ends at the entrance of the vestibulum. In the anterior three-quarters of the vestibulum the cilia are curved at their free ends and fused at their bases. The wave of movement starts at the anterior end and passes towards the gullet. In the last quarter of the vestibulum the cilia are longer and beat quickly towards the gullet. The undulatory motion of the cilia of the oral groove appears to form four waves in the whole circumference. The gullet is devoid of any cilia. The food vacuoles arise near the fundus of the gullet and then move peripherally in spirals. When stained *intra vitam* with neutral red (1 : 5000 in distilled water) the food vacuoles take the stain in 5 min. The young vacuoles stain yellowish and later on become pinkish. This shows a change in the pH content of the food vacuoles from basic to acidic, i.e. at a rough estimate initially at pH 8 or more to pH 7·5 or thereabout. The food vacuoles are mostly in the anterior half of the body. The food of the ciliate consists of desquamated epithelial cells and erythrocytes of the host fish. Diller (1928) states that *Trichodina* on the gills of tadpoles feed only on bacteria.

The contractile vacuole is 6·0–11·5 μ in diameter and situated near the vestibule (Fig. 1*a*). It pulsates every 30–35 sec. In *T. urinicola*, Fulton (1923) records that the pulsation is very sluggish, while in *T. pediculus* Ehrb., Mueller (1937) records the pulsation at the interval of 10–12 sec. The opening of the vacuole is not clear in the living or fixed specimens, but in sections it can be seen as a very thin short duct opening in the anterior part of the vestibulum. When the organism is stained *intra vitam* the vacuole does not take any stain.

No accessory vacuoles are present in any species of *Trichodina* such as have been reported for *Cyclochaeta domerguei* (Wallengren) by MacLennan (1939) and in various vorticellids by Fauré-Fremiet (1925).

The macronucleus is situated in the posterior half of the body, is horseshoe-shaped, and lies parallel to the plane of the 'skeletal complex' (Figs. 1*a*; 2*a*). It is 6·0–10·5 μ thick in the centre and somewhat thinner at the ends. The two ends of the nucleus are separated by the vestibulum and the contractile vacuole. The micronucleus is situated in a pocket in the macronucleus on its outer edge and can be seen only in the sections. During vegetative life the macronucleus is uniformly granular.

The body of the ciliate is covered by a thin protoplasmic pellicle. Within this is the dense granular layer of the protoplasm. The endoplasm is less granular and has many food vacuoles and the contractile vacuole.

LOCOMOTION

The organism moves by the help of the posterior cilia. Each cilium moves with a gyratory motion while the resultant movement of the whole ring appears as a wave motion. The animal rotates in a clockwise or anti-clockwise direction and moves very quickly with the posterior end forwards when swimming freely in water. There does not seem to be any relation between gyratory and rotatory motion. During movement the body is very much constricted antero-posteriorly and the velum increases in size. When the animal is 'browsing' on the gill with its adhesive disk in contact with the gill surface, it does not move very quickly.

PATHOGENIC EFFECT

When *Trichodina* settles on the gills and makes itself secure by the application of the adhesive disk then considerable local irritation must be caused, and this seems to bring about the desquamation of the epithelial cells of the gills. No very marked pathogenic effect was observed on the gills of the fishes examined during the course of the present studies, though there is no doubt that considerable harm could be done to the host if the ciliates were present in large numbers. At times, in fresh-water fish hatcheries, some species of *Trichodina* cause epidemic mortality.

REPRODUCTION

As a rule in the family Urceolaridae reproduction is by binary fission, though conjugation and endomixis also take place. Some stages of fission have been observed in *T. branchicola*. Preparatory to the fission the macronucleus becomes round and then oblong and stains deeply with haematoxylin. The shape of the organism changes and it too becomes oblong and later on dumb-bell-shaped. The micronucleus divides into two and can be seen lying on the outside of the macronucleus (Fig. 2*d*). There is a constriction in the adhesive disk, and then in the denticulate ring. The macronucleus and the whole body then divide into two daughter individuals.

The young individual has about half the adult number of the denticles in the denticulate ring. The old vestibulum persists in one of the daughter individuals while a new one seems to develop in the other. Peshkowsky (1923) states that the oral cilia, gullet and contractile vacuole are absorbed during division in *T. mitra* and *T. steinii*. Padnos & Nigrelli (1942) report that these organs definitely remain in *T. spheroidesi* during the fission, as occurs in the present species. The fate of the contractile vacuole could not be followed, though according to Padnos & Nigrelli it cleaves at the same time as the macronucleus in *T. spheroidesi*. Diller (1928) states that the contractile vacuole probably persists in one of the daughter individuals in *Trichodina* sp. on the gills of tadpoles.

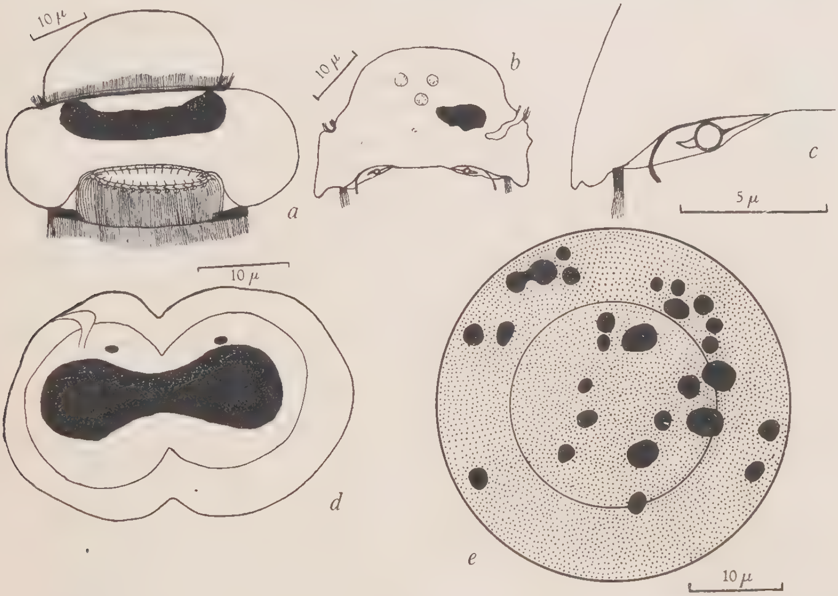

Fig. 2. *Trichodina branchicola*: *a*, side view; *b*, vertical section showing food vacuoles and oral groove; *c*, portion of the same showing skeletal complex in section; *d*, individual undergoing fission, showing macro- and micro-nuclei and a part of the oral groove; *e*, macronucleus broken up into small fragments.

The young individual has the shape of the adult. The 'skeletal complex' arises *de novo* in the adult exterior to the smaller skeletal complex inherited from the parent which is gradually absorbed. Various stages in the development of the new denticulate ring are seen and they confirm fully the findings of Fauré-Fremiet & Thareaux (1944, pl. 1, figs. 1–5). At first the central cone is formed, then the outer hook and lastly the inner ray. At first the denticle is thin but gradually it becomes thick. The young individuals, with one ring only, measure 25–33 μ in diameter, the diameter of the denticulate ring being 6·5–10 μ. The number of denticles is 10–13. The macronucleus is round or

TABLE II. SUMMARY OF DATA ON ALL *TRICHODINA* SPECIES

Measurements (of diameter and height) in μ

Species	No. of denticles	No. of striae per denticle	Total diam.	Diam. of striated ring	Diam. of denticulate ring	Height	Habitat	Host	Habitat of host
ENDOPARASITES:									
T. urinicola Fulton, 1923	26–36	—	—	—	34–35	—	Urinary bladder	*Triton cristatus*, *Bufo* sp.	Fresh water
T. okajimae Ibara, 1931	34–38	—	40–60	20–40	—	45–70	,,	*Hynobius tokyoensis*	,,
T. [*V.*] *renicola* (Mueller, 1931) n.comb.	56	—	70–96	—	—	—	,,	*Esox niger*	,,
T. [*V.*] *nephritica* (Mueller, 1938) n.comb.	36–40	10	—	62–75	—	—	,,	*Esox masquinongy*	,,
T. vesicularum Fauré-Fremiet, 1943	21–33	—	50	—	19–22	—	,,	*Triton cristatus*, *T. palmatus*	,,
T. fariai Da Cunha & Pinto, 1928	24–28	—	40	—	20–42	32	Intestine	*Spheroides testudineus*	Marine
ECTOPARASITES:									
T. labrorum Chatton, 1910	21	—	30–34	—	—	18–22	Gills	*Symphodus tinca* and *S. melops*	,,
T. chelidonichthys Fantham, 1930	30	—	30–45	19–32	—	19–27	,,	*Chelidonichthys cupensis*	,,
T. mugilis Fantham, 1930	32	—	33–34	23–28	—	14–20	,,	*Mugil capito*	,,
T. blennii Fantham, 1930	24–32	5	40–45	24–27	—	20–32	Gills and pericardium	*Blennius cornutus*	,,
T. clini Fantham, 1930	24	—	37	20	—	20	,,	*Clinus anguillaris*	,,
T. halli Padnos & Nigrelli, 1942	26–34	—	45–86	41–81	30–54	—	Gills and skin	*Spheroides maculatus*	,,
T. spheroidesi Padnos & Nigrelli, 1942	21–31	—	17–54	18–32	14–22	12–42	,,	,,	,,
T. branchicola n.sp.	20–26	6–8	30–54	19–33	10–20	22–36	Gills	See p. 440	,,

T. pediculus Ehrenberg, 1838	16–26	—	60	—	—	—	Body surface and gills	Various fresh-water fishes, tadpoles and salamanders; *Hydra fusca*, *H. viridis*	Fresh water
T. steinii Clarapede & Lachmann, 1858	21–26	—	40	—	—	40	Body surface	*Polycelis nigra*, *Dugesia lugubris*, *Polycelis cornuata*	,,
T. [*C.*] *spongillae* Jackson, 1875, n.comb.	37	—	*c.* 61–60	—	—	—	Inside the body	*Spongilla fluviatilis*	,,
T. [*C.*] *domerguei* (Wallengren, 1897), n.comb.	18–25	—	23–56	—	—	$\frac{1}{6}$th of diameter	Gills	On various fishes	,,
T. truttae Mueller, 1937	28–31	20	120–140	110–125	75–85	—	,,	*Salmo clarkii*	,,
T. myakkae Mueller, 1937	17–24	4–5	—	21–25	11–12	—	,,	*Aplites salmoides*, *Ictiobus bubalus*, *Carpoides carpio*, *Salvalinus fontinalis*	,,
T. [*C.*] *guberleti* MacLennan, 1939, n.comb.	28–32	—	50–100	—	—	25	Gills and skin	*Richardsonius balteatus*, *Apocope oscula carringtoni*	,,
T. tenuidens Fauré-Fremiet, 1943	27–37	—	—	—	—	41–55	,,	*Gasterosteus aculeatus*	,,
T. discoidea Davis, 1947	18–30	6–8	—	35–50	19–29	—	Gills	*Lepomis macrochirus*, *Pomoxis sparoides*, *Ambloplites rupestris*, *Ictalurus punctatus*	,,
T. platyformis Davis, 1947	26–35	10	—	56–75	31–50	—	,,	*Margariscus margarita*, *Rhinichthys atronasus*	,,
T. vallata Davis, 1947	18–21	10	—	38–48	25–30	—	,,	*Ictalurus punctatus*	,,
T. fultoni Davis, 1947	25–30	12–14	100	75–90	50–58	—	,,	*Huro salmoides*, *Micropterus dolomieu*, *Lepomis macrochirus*, *Ambloplites rupestris*, *Salmo irideus*	,,
T. symmetrica Davis, 1947	21–28	5	—	24–35	13–22	—	,,	*Ictalurus punctatus*, *Margariscus margarita*, *Rhinichthys atronasus*	,,
T. californica Davis, 1947	25–32	8–10	—	38–50	25–33	—	,,	*Oncorhynchus tschawytscha*	,,
T. tumefaciens Davis, 1947	19–26	7	—	29–30	18–23	—	,,	*Cottus bairdii*	,,
T. bulbosa Davis, 1947	19–24	5–6	—	22–26	10–12	—	,,	*Margariscus margarita*	,,
T. brusiformis Davis, 1947	24–27	5	—	25–35	14–18	—	,,	*Ambloplites rupestris*	,,

ellipsoidal at first but gradually becomes horseshoe-shaped. No stages of conjugation were observed. I have found one individual in which the nucleus is broken up into small spherules (Fig. 2*e*) and is very much like the fig. 14, pl. II of Padnos & Nigrelli (1942) and figs. 29–36, pl. 3 of Diller (1928). In the absence of other stages it is very difficult to interpret correctly the nucleus phase of this individual.

The rate of fission during the summer increases, for it is only during the months of March to August that various individuals undergoing fission were observed. No quantitative population count was done to find the percentage of the dividing forms. Only one young individual was observed during the period September 1946–March 1947, while several have been observed from April 1947 to August 1947.

Discussion on Taxonomy

Fauré-Fremiet (1943) has recently given a very good systematic review of the family Urceolaridae. He retains only two genera, *Trichodina* Ehrb. and *Urceolaria* Stein., in this family; and he relegates the genus *Cyclochaeta* Jackson as a sub-genus of *Trichodina*, and *Leiotrocha* Fabre-Domergue as a sub-genus of *Urceolaria*.

The members of the genus *Trichodina* are generally found as ectoparasites on the gills and skin of fishes and tadpoles, and as endoparasites in the urinary bladder of fishes and Urodela and rarely in Anura. Mueller (1938) has created a new genus *Vauchomia* for endoparasitic urceolarids. The only difference between *Vauchomia* and *Trichodina*, according to Mueller, is that the former has a system of 'myonemes' and the oral groove makes more than two turns. The shape of the denticulate ring is similar in both these genera. The 'myonemes' have, however, since been described in additional species of ectoparasitic *Trichodina*. The distinction, therefore, does not strictly hold, and the name *Vauchomia* is relegated to a synonym of *Trichodina*.

In distinguishing the different species of the genus *Trichodina* (which now includes *Cyclochaeta* and *Vauchomia* as well) the size, shape and the number of the denticles are of great value. Fauré-Fremiet (1943, p. 163) and Davis (1947, p. 7) have also emphasized this point. Biometrical studies on the variation in the number of denticles in a population of *Trichodina* are of great help in finding out whether that particular population contains one or two species of *Trichodina*. Mueller (1937) pointed out that Wallengren (1897) was probably dealing with more than one species of *Trichodina* which he described as *T. pediculus*. Recently Fauré-Fremiet (1943), on the basis of his biometrical studies, has pointed out that there are really two species of *Trichodina* on the skin of *Gasterosteus aculeatus*. The one with 20–26 denticles is *T.* [*Cyclochaeta*] *domerguei* (Wallengren), and the other with 30–34 denticles he named *T. tenuidens*. The variation in the number of denticles is the same in *T.* [*Cyclochaeta*] *domerguei* and *T. branchicola* n.sp., but the size of the denticles and the shape of the body differ in the two species.

At present there are 31 species of *Trichodina* out of which 16 are freshwater, 8 marine, 6 endoparasites in the urinary bladder, and one in the intestine of *Spheroides testudineus*. In Table II the measurements, habitats and hosts of all the species of *Trichodina* are given.

I take this opportunity to thank the Director and the Staff of the Plymouth Laboratory for their kind interest and facilities offered to me. My hearty thanks are due to Miss N. G. Sproston, under whose guidance this work was done, for her helpful criticisms and encouragement, and to Miss T. Skilton for her help in translating the French papers.

SUMMARY

The morphology and reproduction of *Trichodina branchicola* n.sp. are described. Its total diameter is 30–54 μ, and its height is 20–36 μ; the diameter of the striated ring is 19–33 μ, and the diameter of the denticulate ring 10–20 μ. There are 20–26 denticles in the ring, with 6–8 striations to each denticle. The denticles measure 1·5–2 μ in thickness, 3·5 μ in length, each with a broad outer hook 2·3 μ long and an inner ray 3·2 μ long. The aboral cilia are fused at their base to form a complete membranelle.

This organism is found on the gills of the following marine fishes at Plymouth: *Ciliata mustela*, *Gaidopsaurus tricirratus*, *Cottus bubalis*, *Spinachia spinachia*, *Blennius pholis*, *B. guttorugine*, *Trigla lucerna* and *Pleuronectes platessa*.

The genus *Vauchomia* Mueller 1938 is regarded as a synonym of *Trichodina*.

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METHODS OF IDENTIFICATION OF THE LARVAE OF *BALANUS BALANOIDES* (L.), *B. CRENATUS* BRUG. AND *VERRUCA STROEMIA* O. F. MÜLLER

By K. A. Pyefinch

Biologist, The Corrosion Committee, British Iron and Steel Research Association.
From the Marine Station, Millport

(Text-figs. 1–6)

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Introduction

A review of the literature on barnacle larvae suggests that the information available falls roughly into two categories. A number of accounts are now available which give detailed descriptions of the full sequence of larval stages for a particular species. Willemoes-Suhm (1876) described the larval stages of *Lepas fascicularis*; Groom (1894) those of *Balanus perforatus*; Herz (1933) the larval stages of *B. crenatus*; Kühnert (1935) the larval stages of *Alcippe lampas*; Bassindale (1936) those of *Balanus balanoides*, *Chthamalus stellatus* and *Verruca stroemia*; Yasugi & Ishida (1937) the free-swimming stages of *Balanus amphitrite albicostatus*; and Batham (1946) the larval stages of *Pollicipes spinosus*. As well as these fuller accounts, a number of references are available which describe and figure some of the larval stages; these range from the more comprehensive accounts of Hoek (1909) and Nilsson-Cantell (1921), through shorter accounts in papers dealing more specifically with other topics (e.g. Runnström, 1925, 1926; Lochhead, 1936), to brief descriptions of unidentified material (e.g. Stubbings, 1940).

Barnacle larvae, both nauplii and cyprids, are prominent components of the zooplankton in early spring and none of the sources of information just mentioned provides a means of rapid identification which would enable species and stages to be recognized when working through a plankton haul. Because of this difficulty, many workers have had to be content with recording the presence of Cirripede larvae without attempting further identification (e.g. Lebour, 1917; Marshall, 1925), others have made tentative identifications based on the identity of the commonest barnacles on the neighbouring shore (e.g. Moore, 1935), or on a knowledge of the spawning seasons of shore barnacles of the area studied (e.g. Fish, 1925).

In the course of biological work carried out in connexion with research on the fouling problem, studies have been made on the barnacle larvae occurring in the plankton at Millport. It has proved possible to discover characteristics which are sufficiently clear to be recognized at a glance under a low-power binocular microscope, and which therefore enable the species and, to a considerable extent, the stage of barnacle larvae to be identified *in situ* in a dish of plankton.

The larvae of *Balanus balanoides*, *B. crenatus* and *Verruca stroemia* form the chief constituents of the Cirripede larvae in the plankton at Millport, and in this paper attention will be confined to methods for recognizing the larval stages of these three species. Other Cirripede larvae occur in much smaller numbers, in particular the nauplius of a species of *Sacculina* (probably *S. carcini*), the nauplius of a species of *Peltogaster* and nauplii and cyprids which may be those of *Balanus porcatus*. All these can be distinguished from the larval stages of the three species first mentioned, but knowledge of their appearance is too fragmentary to warrant their inclusion in the scheme set out below.

That the larval stages of only three species should be common in plankton hauls taken at Millport imposes, it is recognized, a disadvantage on the identification scheme set out later. Though these larval stages are fairly readily distinguishable *inter se*, some of them may resemble the larval stages of other species of barnacles, not present on the Clyde, so closely as to make this scheme difficult to use elsewhere. Inspection of the published figures of other species of barnacles does not suggest any obvious difficulties in this respect, but reasonable certainty that the characteristics suggested below are truly distinctive must await further work on the larvae of other species.

The Characteristics of the Larval Stages

Balanus balanoides, *B. crenatus* and *Verruca stroemia* each pass through six naupliar stages before reaching the cyprid stage. Herz (1933) has described eight naupliar stages for *Balanus crenatus*, but Bassindale (1936), after reviewing the evidence put forward by Herz, concludes that 'it seems possible to regard the number of stages as not being perfectly established'. The present author has reared *B. crenatus* in the laboratory and has not been able to discover more than six naupliar stages so that it would appear that *B. crenatus* at Millport agrees with *B. balanoides* in possessing the same number of naupliar stages.

Outline diagrams of the six naupliar stages of *B. balanoides* are shown in Fig. 1; these will be used to illustrate the characteristic features of each of these

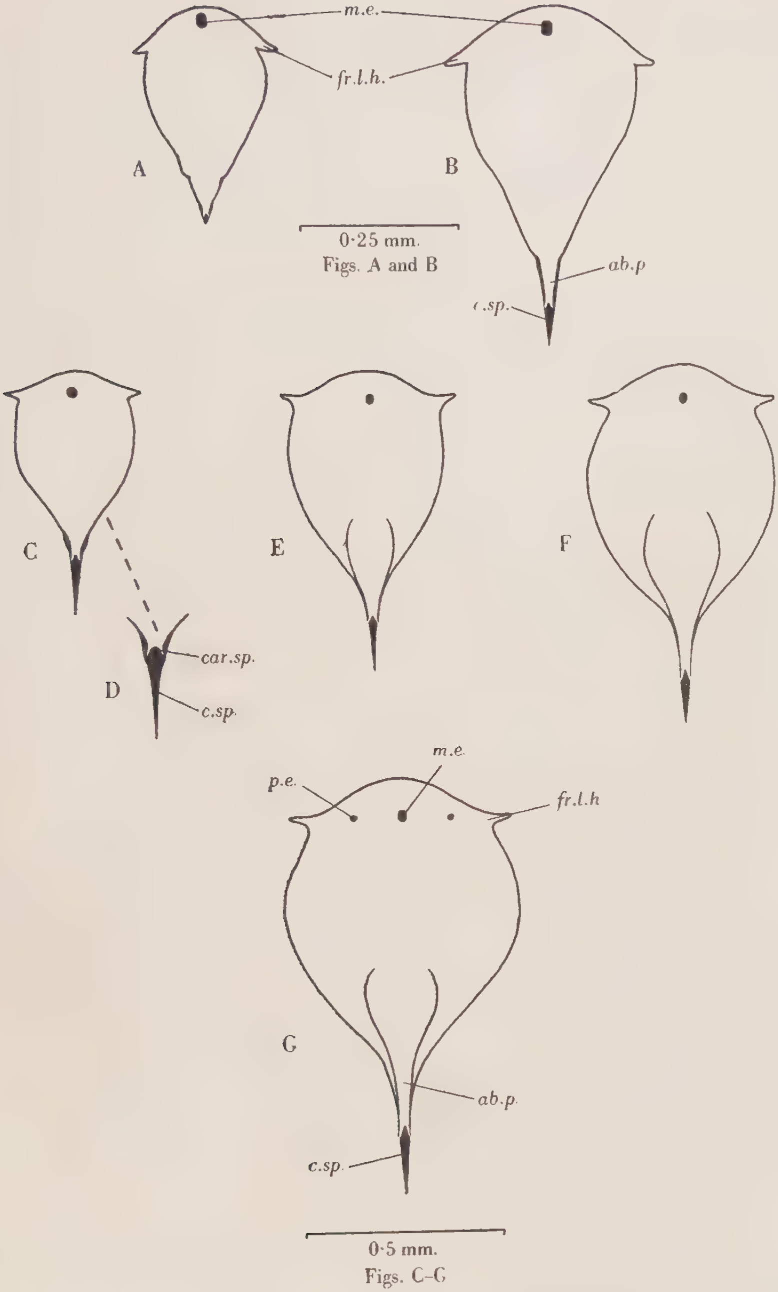
m.e.
fr.l.h.
A
B
0·25 mm.
Figs. A and B
ab.p
c.sp.
C
D
car.sp.
c.sp.
E
F
m.e.
p.e.
fr.l.h
G
ab.p.
c.sp.
0·5 mm.
Figs. C–G

Fig. 1. Outline diagrams of the six naupliar stages of *Balanus balanoides* in ventral view. A, first-stage nauplius; B, second stage; C, third stage; D, dorsal view of hinder edge of carapace of third-stage nauplius, showing carapace spines; E, fourth stage; F, fifth stage; G, sixth-stage nauplius. *ab.p.*, abdominal process; *c.sp.*, caudal spine; *car.sp.*, carapace spine; *fr.l.h.*, fronto-lateral horn; *m.e.*, median eye; *p.e.*, paired eye.

stages. The larvae are liberated from the mantle cavity of the parent as *first-stage nauplii* (Fig. 1 A). These are characteristically pear-shaped in outline and the short fronto-lateral horns point obliquely backwards. These horns are clearly discernible at this stage, but they become more prominent in the later naupliar stages. The characteristic feature of the first-stage nauplius, however, is the form of the posterior end which is blunt, as the posterior processes, which are conspicuous features of later naupliar stages, are barely developed in the first-stage larva.

The first moult seems to take place very shortly after hatching. Bassindale (1936) has briefly discussed the estimates that have been made of the length of life of the first naupliar stage and all that need be added here is that, for *B. balanoides*, observations on cultures of the larvae and plankton studies both suggest that the first moult occurs for this species within 24 hr. after liberation. In the *second-stage nauplius*, which emerges from this moult, the fronto-lateral horns are more conspicuous and the posterior processes are much better developed. There are two processes projecting posteriorly, one situated dorsally and the other ventrally. These processes have been named in various ways by various workers; the dorsal process has been termed the caudal spine (Groom, 1894; Nilsson-Cantell, 1921; Runnström, 1925; and Bassindale, 1936), the caudal process (Lochhead, 1936) or the carapace spine (Hoek, 1909); and the ventral process has been termed the spinous process (Groom, 1894), the ventral abdominal process (Hoek, 1909; Nilsson-Cantell, 1921; and Runnström, 1925) or the caudal process (Bassindale, 1936; Lochhead, 1936). The term thoracico-abdominal process as used by Herz (1933) evidently applies both to the dorsal and to the ventral processes. In the present account the term caudal spine will be used for the dorsal process, and the term abdominal process for the ventral process. In *B. balanoides*, as in the other two species discussed in this paper, the abdominal process is forked at its tip, whereas the caudal spine is unforked. The form and relationship of these two processes is discussed in the next section.

The moult which ends the life period of the second-stage nauplius seems to be one of the critical periods in the larval life history, since it appears to be the general experience of those who have reared barnacle larvae in the laboratory that most cultures die out before completing this moult, and those cultures in which it is successfully completed usually pass on through the remaining larval stages without further difficulty.

The form of the *third-stage nauplius* (Fig. 1 C) is generally similar to that of the second stage, though the fronto-lateral horns now project roughly at right angles to the long axis of the body. The chief distinguishing feature of this stage is the form of the carapace. In the earlier naupliar stages the carapace has no definite posterior margin, but is produced without interruption into the caudal spine. In the third-stage nauplius, however, the posterior border of the carapace is distinct and is further marked by the presence of two short, simple spines each of which projects backwards a short distance on each side of the mid-dorsal line (Fig. 1 D). These spines, which occur in the later naupliar stages both of *B. balanoides* and *B. crenatus*, are here termed carapace spines. In his diagrams of the outlines of the six naupliar stages of *B. balanoides* Bassindale (1936, fig. 2A, p. 59) does not figure these carapace spines, though he indicates the definite posterior margin of the carapace. They are present, however, in third-stage *B. balanoides* nauplii from the Clyde.

It is not at first easy to distinguish the *fourth- and fifth-stage nauplii* (Fig. 1 E, F) from the third-stage larvae, as the main difference between these three stages is one of size. If they occur together in a plankton haul (as frequently happens) distinction is not difficult, as the fifth-stage nauplius is roughly half as long again as the third-stage larva, but if only one stage occurs or if the numbers present are small, it may be necessary to measure individual larvae to check their stage. Practice, however, soon enables any one of these three stages to be recognized even if the other stages are not available for comparison. The swollen base of the abdominal process (within which the rudiments of the post-mandibular appendages can be discerned) helps to distinguish the fourth- and fifth-stage nauplii from the third stage, since this swelling first becomes obvious in the fourth-stage nauplius and is prominent in the succeeding stage. A careful examination of the third-stage nauplius, however, shows that the base of the abdominal process is slightly swollen in this stage also, so that this character is not diagnostic.

Finally, the *sixth-stage nauplius* (Fig. 1 G) can be recognized by the appearance of the paired eyes. The median eye, which has been present throughout the larval sequence, also persists in the sixth-stage nauplius. When the paired eyes are fully pigmented they are immediately obvious but it would seem that pigmentation proceeds slowly, probably during the life period of this naupliar stage, as some nauplii occur in which pigmentation is only just beginning and others in which the pigment is distinctly red in colour. When fully developed the pigment is black. This gradual development of pigmentation in the sixth-stage nauplius is found not only in *B. balanoides*, but also in the corresponding stage of *B. crenatus* and *Verruca stroemia*.

It is more convenient to reserve a description of the characteristic features of the *cyprid larva* for the next section, where it will be compared with the corresponding stage of the other two species under discussion.

DISTINCTIONS BETWEEN THE LARVAE OF *BALANUS BALANOIDES*, *B. CRENATUS* AND *VERRUCA STROEMIA*

Second-stage nauplii. Comparisons of the naupliar stages of *Balanus balanoides*, *B. crenatus* and *Verruca stroemia* can most profitably be made, in the first instance, between the second-stage nauplii. This is the most convenient stage for this purpose for two reasons: second-stage nauplii are those most frequently encountered in tow-nettings, and at this stage the main specific characteristics

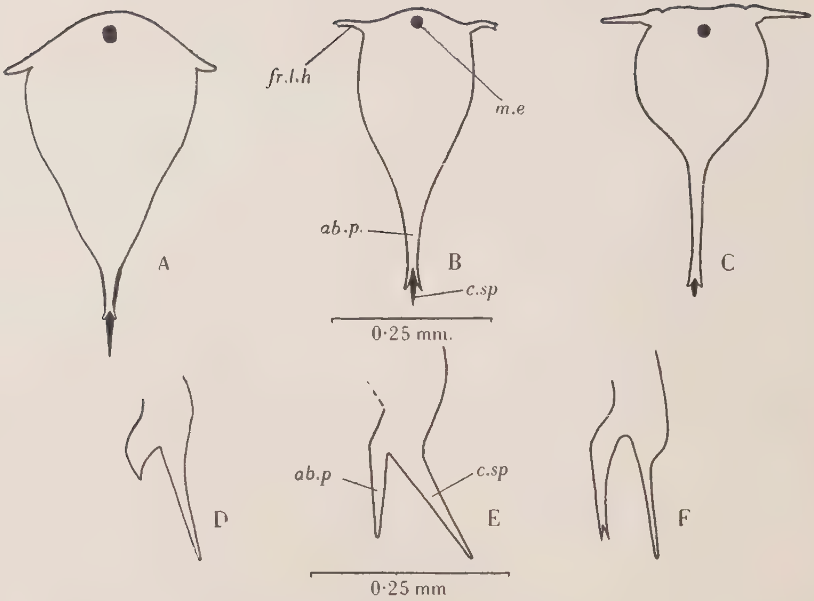

Fig. 2. Second-stage nauplii of (A) *Balanus balanoides*, (B) *B. crenatus*, and (C) *Verruca stroemia*, in ventral view; (D) *Balanus balanoides*, (E) *B. crenatus*, and (F) *Verruca stroemia*, lateral view of abdominal process and caudal spine. *ab.p.*, abdominal process; *c.sp.*, caudal spine; *fr.l.h.*, fronto-lateral horn; *m.e.*, median eye.

TABLE I. CHARACTERISTICS OF THE SECOND-STAGE NAUPLIAR LARVAE

Character	*Balanus balanoides*	*Balanus crenatus*	*Verruca stroemia*
General shape (in ventral view)	Pear-shaped	Triangular	Circular
Anterior margin	Curved	Curved, but radius of curvature greater than that of *B. balanoides*	Almost straight
Fronto-lateral horns	Short, pointing posteriorly	Moderately long, slightly curved, projecting roughly at right angles to main axis	Long and slender, projecting at right angles to main axis
Posterior processes	Caudal spine much longer than abdominal process	Caudal spine longer than abdominal process	Caudal spine either slightly longer than, or equal in length to, abdominal process
	Terminal fork of abdominal process with rami practically parallel	Terminal fork of abdominal process with rami making a distinct angle with each other	
	In lateral view, abdominal process tap-like in form	In lateral view, abdominal process slender, diverging markedly from caudal spine	In lateral view, abdominal process and caudal spine practically parallel, or with former inclined towards latter

are apparent so that a means of recognizing the identity of the second-stage nauplii provides a useful basis for distinguishing the specific identity of later stages.

Fig. 2A–C shows outline diagrams of these second-stage nauplii seen in ventral view, and Fig. 2D–F shows the characteristics and relationships of the caudal spine and the abdominal process, as seen in lateral view. With these diagrams as illustrations, the distinguishing features of these nauplii can be listed as in Table I.

Using these characters, it is possible to recognize this stage of each of the three species under discussion virtually at a glance and distinction is further aided by the existence of other differences, less capable of precise description, but equally valuable as guides to identification. For example, the larvae of *Balanus balanoides* give an impression of bulk (this applies to all the naupliar stages, not only to the second stage) which produces a clumsy appearance, whereas the larvae of *B. crenatus* and *Verruca stroemia* are delicate and more transparent in appearance.

Later nauplii. Once the second-stage nauplii can be distinguished, the recognition of the specific identity of the later naupliar stages is not difficult as the main characteristics of the second-stage nauplii persist through the later naupliar stages, but there are a few complications which may cause some difficulty and therefore deserve mention.

The short, tap-like abdominal process of the second-stage nauplius of *Balanus balanoides* does not wholly retain this form through the later larval stages, since it becomes more elongated relative to the caudal spine. In the third-stage nauplius the ratio of the length of the caudal spine to that of the abdominal process is 3:1, but in the sixth-stage nauplius it has become 1·7:1. As this ratio for the sixth-stage nauplius of *B. crenatus* is of the order of 1·3:1 and as the abdominal process of the latter stage does not diverge so sharply from the caudal spine as in its second-stage larva—possibly owing to the swelling of the base of the abdominal process (see Fig. 3C), an examination of the posterior region of the larvae in lateral view may not be very helpful. Distinction can be made, however, on the basis of general appearance, the form of the forked tip of the abdominal process and the dorsal outline. The later naupliar stages of *B. balanoides* fully retain the bulky appearance of the earlier stages and the tissues of formalin-preserved specimens often appear particularly dense, whereas the corresponding stages of *B. crenatus* retain their delicacy and transparency. The rami of the forked tip of the abdominal process of *B. balanoides* remain more parallel than those at the tip of the abdominal process of *B. crenatus* (Fig. 3B, D), and the dorsal edge of the carapace is much more rounded in *B. balanoides* than it is in *B. crenatus* (Fig. 3A, C).

The series of structural changes in the sequence of nauplii of *Verruca stroemia* is not quite the same as that of the nauplii of *Balanus balanoides* and *B. crenatus*. In the latter the third-stage nauplius can be distinguished from the earlier stages by the definite posterior margin of the carapace which bears the carapace spines. In *Verruca stroemia* the carapace does not acquire a definite posterior margin until the fourth-stage nauplius and this margin lacks carapace spines, both in this and in the two succeeding naupliar stages (see Fig. 4). In *V. stroemia*, therefore, the fourth-stage nauplius is readily distinguished from the third stage, but the distinction between the second and third stages seems to be one of size only. Third-stage nauplii of *V. stroemia* do

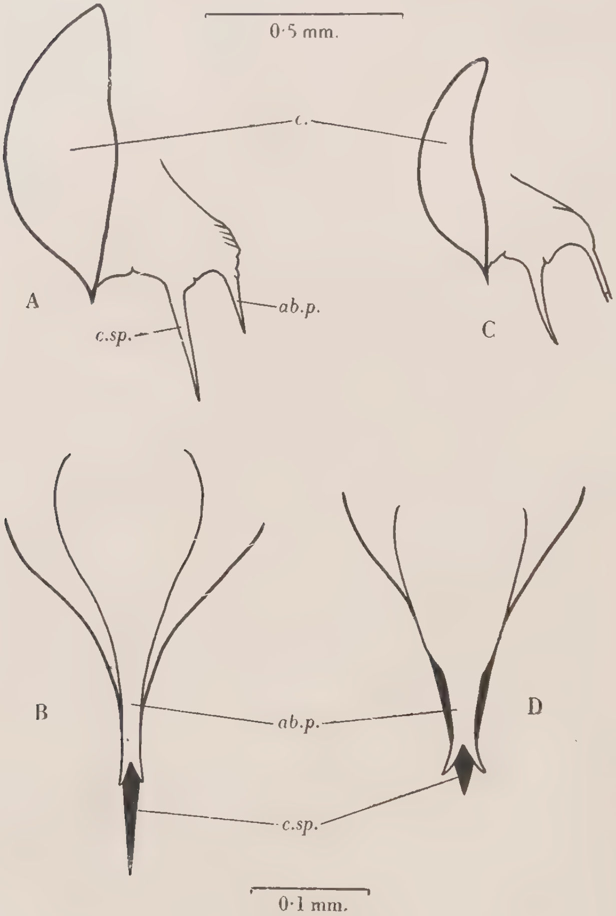

Fig. 3.

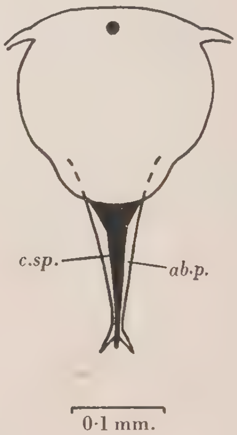

Fig. 4.

Fig. 3. Sixth-stage nauplii of (A, B) *Balanus balanoides*, and (C, D) *B. crenatus*. Above, lateral view of nauplius; below, posterior processes enlarged in ventral view. *ab.p.*, abdominal process; *c.*, carapace; *c.sp.*, caudal spine.

Fig. 4. Dorsal view of the fourth-stage nauplius of *Verruca stroemia*. The absence of carapace spines should be noted.

not seem to occur at all commonly in plankton hauls made at Millport, though Bassindale (1936) found this stage to be that which occurred most commonly in his cultures of the nauplii of this species.

Details of the lengths of the naupliar stages of the three species are given in Table II. Those for *Balanus balanoides* and *Verruca stroemia* are compared with those given by Bassindale (1936), which are given in parentheses below the measurements recorded in the course of the present survey. The range of variation in the length of these larvae from one place to another is unknown but in view of the known differences in size between cyprids of *Balanus balanoides* from different latitudes (see p. 461), it would seem unwise to place too much reliance on the universal application of length measurements. In the present instance, these measurements are quoted to give an idea of the order of difference in length of the larval stages of the three species.

TABLE II. LENGTHS OF THE NAUPLIAR STAGES OF *B. BALANOIDES*, *B. CRENATUS* AND *V. STROEMIA*

	B. balanoides		*B. crenatus*		*V. stroemia*	
Stage	Full length (mm.)	Carapace length (mm.)	Full length (mm.)	Carapace length (mm.)	Full length (mm.)	Carapace length (mm.)
Nauplius I	0·34 (0·35)	—	0·28	—	— (0·27)	—
Nauplius II	0·54 (0·51)	—	0·44	—	0·40 (0·44)	—
Nauplius III	0·63 (0·62)	0·42 (0·37)	0·57	0·35	0·47 (0·50)	—
Nauplius IV	0·76 (0·69)	0·54 (0·41)	0·73	0·48	0·54 (0·58)	0·31 (0·34)
Nauplius V	0·92 (0·81)	0·63 (0·53)	0·84	0·59	0·62 (0·63)	0·39 (0·37)
Nauplius VI	1·05 (1·15)	0·73 (0·79)	0·91	0·63	0·73 (0·69)	0·47 (0·42)

Measurements in parentheses are taken from Bassindale (1936).

First-stage nauplii. Outline diagrams of the first-stage nauplii of these three species are shown in Fig. 5, from which it will be evident that each differs considerably in appearance from its succeeding stages; this difference is probably least for the first-stage nauplius of *B. balanoides*. The brevity of the posterior processes seems to be the common characteristic of these three first-stage nauplii.

The first-stage larva of *B. balanoides* (Fig. 5A) gives promise of the bulky appearance that has been mentioned as a general characteristic of the later naupliar stages; there is nothing that can be added here to the description given earlier (p. 454). The first-stage larvae of *B. crenatus* (Fig. 5B) and *Verruca stroemia* (Fig. 5C) are, in spite of their evident differences shown in these outline diagrams, curiously easy to confuse when examining a plankton haul.

Though the first-stage nauplius of *V. stroemia* has long, well-developed fronto-lateral horns, in formalin-preserved material these are often obscured by the first antennae, which lie over them (Fig. 5C)—it is interesting to find that this had evidently occurred in the specimen which Nilsson-Cantell (1921) used for his figure of the first-stage nauplius of this species. With the fronto-lateral horns obscured in this way, there is little to distinguish the first-stage nauplii of *V. stroemia* and the corresponding stage of *Balanus crenatus*, in ventral view, except size. This confusion can, however, readily be resolved, for if the first-stage larva of *Verruca stroemia* is turned forwards, by a needle placed under the posterior processes, on to its anterior edge, the fronto-lateral horns are easily seen curving away from the body. Since the fronto-lateral horns of the first-stage nauplius of *Balanus crenatus* are closely bound to the sides of the carapace, this operation does not reveal their presence in this species.

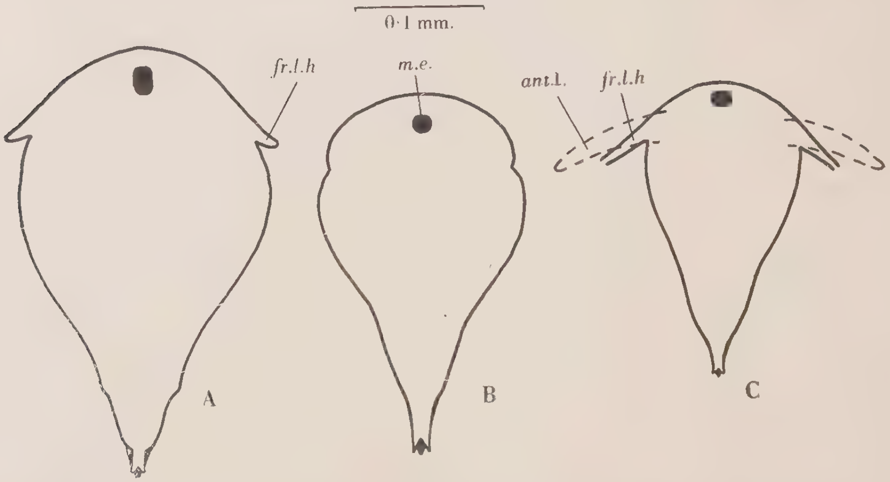

Fig. 5. First stage nauplii of (A) *Balanus balanoides*, (B) *B. crenatus*, and (C) *Verruca stroemia* in ventral view. *ant.*1, first antenna; *fr.l.h.*, fronto-lateral horn; *m.e.*, median eye.

Nilsson-Cantell (1921) has emphasized the case with which liberation of larvae can take place in the laboratory and has stressed the fact that therefore larval stages may occur under aquarium conditions which are not normally liberated under more natural circumstances. It should therefore be added that all the first-stage larvae described in this section have been recovered from plankton hauls in considerable numbers and there is little doubt that these stages are members of the series of stages normally present in the sea.

Cyprids. Diagrams of the outline of the cyprid larvae of these three species, shown in Fig. 6, indicate that there are considerable differences in size between them, the cyprid of *B. balanoides* (Fig. 6A) being the largest, that of *Verruca stroemia* (Fig. 6C) the smallest.

Confusion is most likely to arise between the cyprid of *Balanus balanoides* and that of *B. crenatus*. The specimens chosen for Figs. 6A and 6B may be considered typical specimens of the two species of cyprids, but the limits of variation in length of the cyprids of the two species unfortunately are such that the biggest *B. crenatus* cyprids are as long as, or slightly longer than, the smallest cyprids of *B. balanoides*. Further, the cyprid of *B. balanoides* seems to vary in length with latitude; Runnström (1925) states that this larva is 1·2 mm. long, whereas Bassindale (1936) found specimens collected at Plymouth to be 0·94 mm. in length. Measurements of this cyprid from the plankton at Millport show that the length varied from 0·9 to 1·1 mm., though most lay within the range 0·98–1·06 mm. This suggests that the cyprid of *B. balanoides* attains a greater length in northern waters.

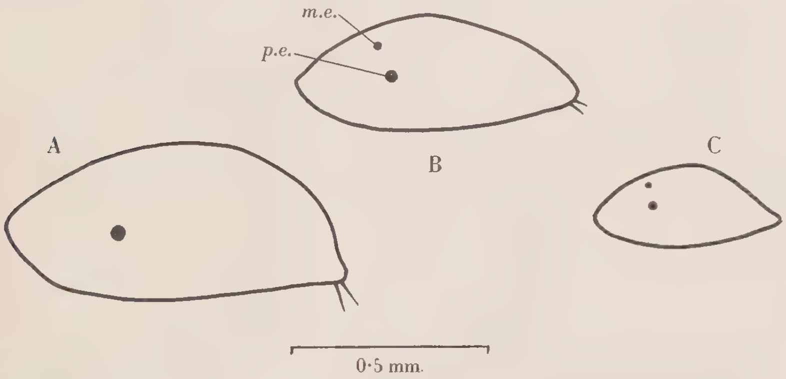

Fig. 6. Cyprid larvae of (A) *Balanus balanoides*, (B) *B. crenatus*, and (C) *Verruca stroemia*. *m.e.*, median eye; *p.e.*, paired eye.

Other characters can, however, be used to distinguish the cyprid of *B. balanoides* from that of *B. crenatus*. Typically, the former is brown in colour, whereas the latter is not coloured in this way. The degree of pigmentation of the cyprid of *B. balanoides* varies considerably, however, and some lightly pigmented specimens may not be easy to distinguish. In these the position of the eyes has proved a useful character. In the cyprid of *B. balanoides* the median eye lies at very much the same distance from the dorsal edge of the carapace, whereas in the cyprid of *B. crenatus* the paired eyes lie at a greater distance from the dorsal edge of the carapace than the median eye. Consequently, in lateral view, only one of the paired eyes can be seen in the cyprid of *B. balanoides* (Fig. 6A), whereas one of the paired eyes and the median eye can be seen in the cyprid of *B. crenatus* (Fig. 6B). The difficulties that may arise in distinguishing these two species of cyprids have been discussed at some length, as experience has shown that awkward specimens do occur, but it should be emphasized that they form only a small fraction of the whole and that it is possible to distinguish *most B. balanoides* cyprids from *most B. crenatus* cyprids at a glance.

One of the paired eyes and the median eye can also be seen when the cyprid of *Verruca stroemia* is seen from one side, but there is little chance of confusing this cyprid with that of *Balanus crenatus* as the difference in size is pronounced. Moreover, the dorsal border of the carapace of the cyprid of *Verruca stroemia* is practically straight posteriorly, whereas that of the cyprid of *Balanus crenatus* is distinctly rounded.

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SUMMARY

A description is given of characters which allow the larval stages of *Balanus balanoides*, *B. crenatus* and *Verruca stroemia* to be identified rapidly.

It is emphasized that the characters used in this method of identification are only valid for these three species *inter se*, further work on similar lines for other species may reveal difficulties not apparent in the present scheme.

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NOTES ON THE BIOLOGY OF CIRRIPEDES

By K. A. Pyefinch

Biologist, The Corrosion Committee, British Iron and Steel Research Association.
From the Marine Station, Millport

(Text-figs. 1–18)

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INTRODUCTION

In the course of some four years' work on the fouling problem opportunities have occurred for observations on the general biology of those barnacles whose larvae occur commonly in the plankton and settle in some numbers on surfaces continuously immersed below experimental rafts at Millport.

In his account of the Crustacea of the Clyde sea area, Scott (1901) recorded the presence of the following six free-living species of Cirripedes: *Balanus porcatus* Costa, *B. crenatus* Brug., *B. balanoides* (Linn.), *B. hameri* (Ascan.), *Verruca stroemia* (O. F. Müll.), and *Scalpellum vulgare* Leach.

Two parasitic forms, *Sacculina carcini* (Thomp.) and *Peltogaster paguri* (Rathke), were also recorded then. In the *Annual Reports of the Scottish*

Marine Biological Association for 1919 and 1920 the records of *Chthamalus stellatus* (Poli), *Lepas anatifera* L. and *L. pectinata* Spengler were added to this list, and more recently Moore & Kitching (1939) have estimated the abundance of *Chthamalus stellatus* on the shores of the Isle of Cumbrae.

Examination of tow-nettings shows that the larvae of *Balanus crenatus, B. balanoides* and *Verruca stroemia* are by far the most common Cirripede larvae in the plankton. The larvae of *Sacculina* occur in small numbers, chiefly from November to March; the larvae of *Peltogaster paguri* have been recorded practically the year round, and on occasions nauplii and cyprids which cannot be referred with certainty to their species have been present; it is possible that these are the larval stages of *Balanus porcatus*.

On submerged surfaces, the most common species have been *B. crenatus* and *B. balanoides*. *Verruca stroemia*, in spite of its abundance in the plankton, has not yet been recorded on a raft-exposed surface. Small numbers of *Balanus porcatus* have settled from time to time, but the remaining species listed as known in the Clyde have been represented only by a single specimen of *Lepas*, which settled on a raft-exposed surface during the summer of 1942. It should be added, however, that the surfaces available for settlement have not, in general, extended for more than about 4 ft. below the water surface, and this factor has probably limited the range of settling species. Further, the surfaces available have all been exposed vertically, a condition which may also have had its effect on settlement.

Under these circumstances, observations have chiefly been limited to *Balanus balanoides*, *B. crenatus* and *Verruca stroemia*; these are the three species principally discussed in this paper.

BALANUS BALANOIDES

Development of Larvae and their Occurrence in the Plankton

Balanus balanoides liberates its larvae at only one period of the year, during the early spring. Elmhirst (1923) states that fertilization of the ova occurs from August to November, and Moore (1935*a*) that fertilization takes place during November at Port Erin. Observations made in the course of the present study show that by the middle of January the ovigerous lamellae within the mantle cavity contain ova in an advanced stage of development. At this time these lamellae are pale yellow in colour and form firm, discrete masses within the mantle cavity. During the later stages of development of the ova, the colour of the ovigerous lamellae gradually darkens, passing from pale yellow, through yellowish brown to brown and dark brown, finally becoming, as the larvae are ready to hatch, virtually black. These colour changes, presumably due both to the absorption of yolk and to the appearance of dark-coloured structures within the developing larva, afford a means of tracing, roughly, the rate at which the later stages of larval development occur.

Fig. 1 shows the results of the examination of a series of small samples of *B. balanoides* (each sample roughly 100 individuals) during January to May 1946, in which the proportion of individuals containing ovigerous lamellae in the five colour stages mentioned in the preceding paragraph are expressed as a percentage of the whole sample. (In Stage 1 of Fig. 1 the ovigerous lamellae are pale yellow, in Stage 5 they are black in colour.) From this figure it is evident that development was well advanced when the observations were started, and that further development took place rapidly, a small percentage of individuals containing larvae ready to hatch first appearing towards the middle of February. The latter group reached its maximum in the population examined on 8 March and thereafter showed a general decline in importance, though 2% of the individuals examined on 1 May contained fully developed larvae. Spent individuals were first evident on 13 March and from then onwards progressively dominated the samples examined. These samples of *B. balanoides* were all collected below mid-tide level, that is, from a level below that termed B 1 by Moore (1935*b*).

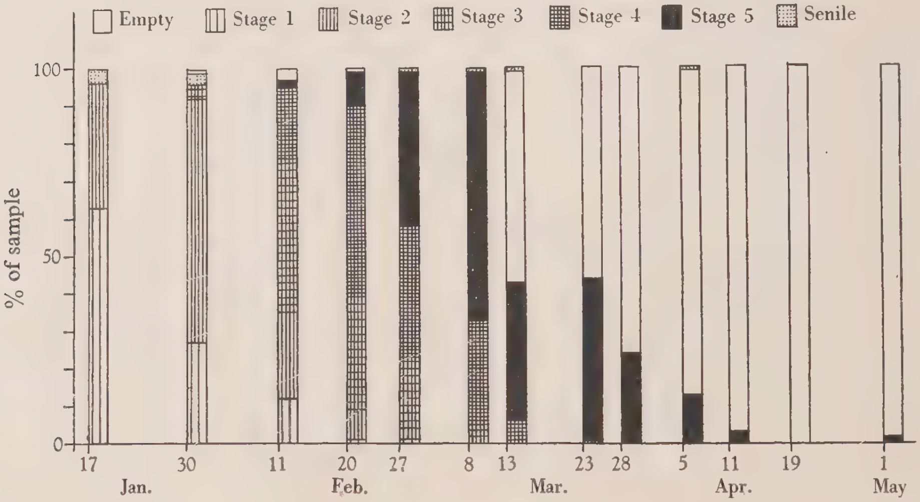

Fig. 1. *Balanus balanoides.* State of development of ova, 1946.

Contemporaneous plankton hauls clearly indicate that the period at which most adults contain larvae ready to hatch corresponds with the appearance of large numbers of 1st and 2nd stage nauplii in the plankton, and suggest that in this species there is a short period when the majority of the adults liberate their larvae. In 1946 the numbers of these larvae present in the plankton were at a maximum on 7 March. Comparable liberations have occurred in the other years covered by these observations: in 1944 the heaviest swarms occurred on 16 March, in 1945 the maximum occurred on 14 March (though numbers were small in comparison with other years), and in 1947 the greatest numbers were present on 11 March, though considerable numbers were present from 5 to 14 March.

Following the methods described in a previous paper (Pyefinch, 1948), it has been possible to trace the appearance and relative abundance of the later larval stages in the plankton, and the results for 1947 are given in Fig. 2. In this figure the average numbers of each stage present, over 3-day periods, have been expressed as a percentage of the total numbers of *B. balanoides* larvae present over each period. These and all other plankton hauls mentioned in this paper have been made from Keppel Pier, Millport; the conditions which allow such hauls to be made from this pier have been described in the *Annual Report of the Scottish Marine Biological Association* for 1922 (p. 7). The nets were fished for 1 hr. daily, starting 1 hr. after high water. Variations in tidal flow between a neap and a spring tide are, of course, considerable and this factor alone makes this method of tow-netting useless for any but the most approximate quantitative comparisons; it is for this reason that the data given in Fig. 2 are presented as percentages rather than as absolute numbers. The latter are too strongly influenced by variations in the speed of tidal flow.[1]

1st and 2nd stage nauplii (which may be considered together because the length of life of the 1st stage is very much shorter than that of the 2nd stage) were first present in small numbers on 20 February, 3rd and 4th stage nauplii first appeared on 4 March, 5th stage nauplii followed on 10 March, 6th stage nauplii on 13 March and the first cyprids were recorded on 22 March. This suggests that roughly 1 month elapses between hatching and the appearance of the cyprid. Moore (1935*a*), quoting Johnstone, Scott & Chadwick (1924), states that 2 months separate the naupliar and cyprid maxima in Port Erin Bay, but as the larval stages were not specifically identified, it is possible that this is an over-estimate, covering more than one species.

The histograms shown in Fig. 2 also suggest that at least three maxima of 3rd and 4th stage nauplii occurred, and indications of corresponding maxima are also present for the 5th and 6th naupliar stages. From the dates of occurrence of these maxima it is possible to make tentative suggestions of the life periods of the naupliar and cyprid stages; for the first two maxima shown in Fig. 2 these appear to be as in Table I.

As these estimates are based on 3-day averages, the shortest possible interval is 3 days. The differences in interval indicated in this table, therefore, with the exception of the interval between the 6th stage nauplius and the cyprid of the first 'brood', probably mean little and it would seem that the length of life of each larval stage is approximately the same, except that of the 1st naupliar stage which, as noted earlier, may be much shorter.

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[1] As an indication of the numbers of larvae taken, the following are the average daily hauls, over the period shown in Fig. 2, for each larval stage: Nauplius I+II, 2430; Nauplius III, 1525; Nauplius IV, 1915; Nauplius V, 870; Nauplius VI, 710; Cyprid, 1750.

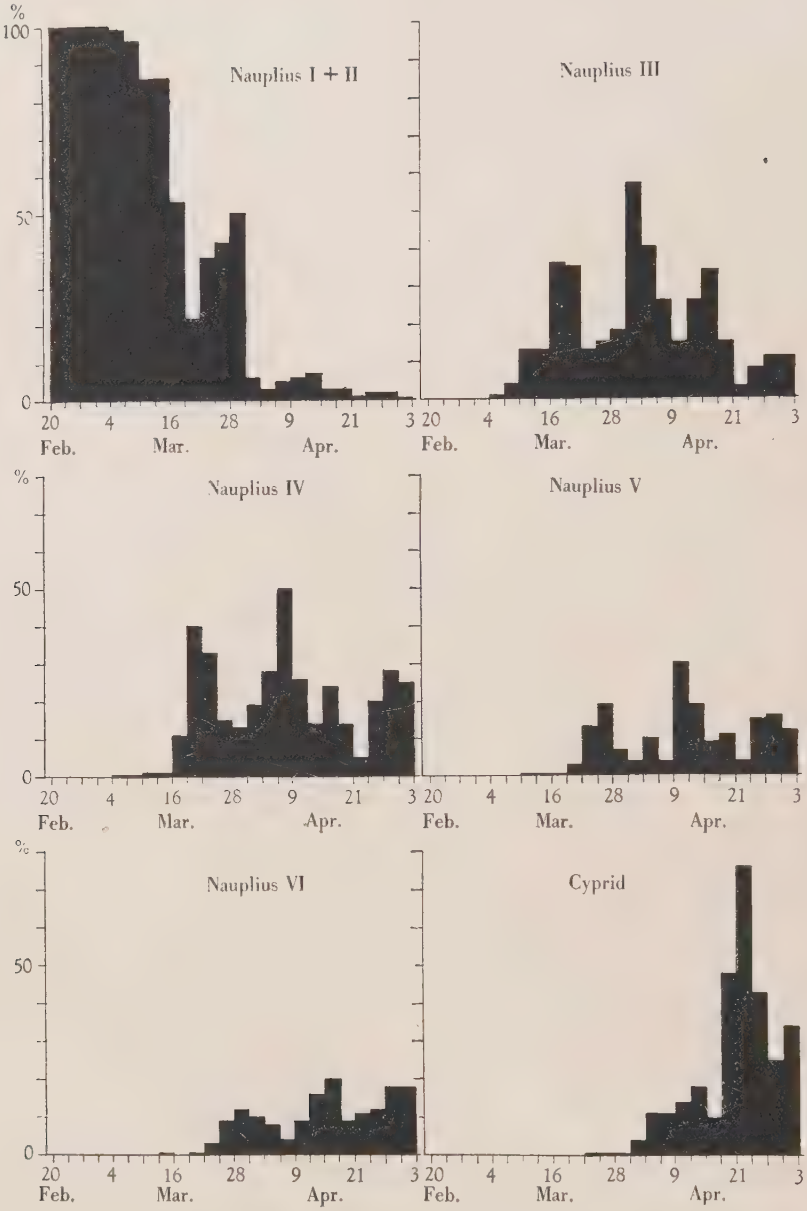

Fig. 2. Occurrence of the larval stages of *Balanus balanoides*, spring 1947. The numbers present, over 3-day periods, of each larval stage are expressed as a percentage of the total *B. balanoides* larvae present.

TABLE I. RATE OF DEVELOPMENT OF *BALANUS BALANOIDES*

Larval stage	Date beginning 3-day period of maximum	Interval (days)	Date beginning 3-day period of maximum	Interval (days)
Nauplius I and II	10. iii.	—	28. iii.	—
Nauplius III	16. iii.	6	31. iii.	3
Nauplius IV	19. iii.	3	6. iv.	3
Nauplius V	25. iii.	6	9. iv.	6
Nauplius VI	28. iii.	3	15. iv.	6
Cyprid	? 12. iv.	? 15	21. iv.	6

The interval between the 6th stage nauplius and the cyprid of the first 'brood' seems almost certainly too long and there are reasons for supposing that it has been caused by the action of other factors, which will be more fully discussed later (see p. 498). For the present it may be mentioned that it seems likely that the first 'brood' of nauplii was relatively unsuccessful, in the sense that they eventually produced only a small proportion of cyprid larvae; in this respect the second 'brood' was much more successful. The numbers of 1st and 2nd stage nauplii involved in the second maximum—that for the period beginning 28 March (Fig. 2)—were only about 35 % of those involved in the first maximum, yet over 45 % of these were recorded in the cyprid stage, whereas under 15 % of the first maximum were so represented. The number of cyprid larvae recorded from the later hatched nauplii was actually slightly greater than that produced from the earlier group.

The length of life of the cyprid stage is difficult to assess. Visscher (1928) states that the free-swimming period of the cyprid lasts from 3 days to 2 weeks or longer. Observations made on the cyprid of *B. balanoides*, taken from the plankton and stored in tanks in the laboratory, suggest that on the average a period of 5 days elapses before settlement begins. Such an estimate, based on artificial laboratory conditions, is not likely to be accurate and field observations suggest that the interval before settlement is much shorter as, when cyprid larvae are present in large numbers in the plankton, settlement on the shore is virtually coincident with the appearance of these swarms.

Visscher (*loc. cit.*) further states that the oil globules, which are present in some numbers in the tissues of the cyprid, particularly towards the anterior end, disappear towards the end of the free-swimming period. It has not been possible to confirm this observation, either for the cyprid of *B. balanoides* or for that of *B. crenatus*. McDougall (1943) states that he has confirmed Visscher's observation for *B. eburneus* but has not found that the oil globules of the cyprid of *Chthamalus fragilis* disappear. Nevertheless, it seems possible that physiological changes do take place during the free-swimming life of the cyprid, changes which must have reached a certain stage before settlement can occur; it is hoped to discuss this point more fully in a later paper.

These notes on the larval stages of *B. balanoides* have chiefly been based on observations made during 1947; the main outline of the story—liberation of larvae during the first half of March, appearance of nauplii of the 3rd and later stages during the second half of that month and first appearance of cyprid larvae late in March or early in April—has been fully confirmed by the observations of the preceding 3 years. The differences between one year and another present some features of general interest, which are discussed more fully later in this paper.

SETTLEMENT AND METAMORPHOSIS

Settlement of the cyprid of *B. balanoides* occurs during April and, over the 4 years covered by this survey, seems to occur most heavily towards the beginning of that month.

Two methods of locomotion are commonly used by the cyprid larva: a swimming motion produced by rapid movements of the thoracic appendages, and a walking motion in which the tips of the antennae are used. It is also of interest to find that the normal response to a slight increase in speed of water movement is one of attachment to the surface; a weak current of water from a pipette can stimulate this clinging reaction and if the water is poured out of a dish or beaker containing *B. balanoides*, the majority of the larvae will remain clinging to the walls of the container. This response is not shown by the cyprid of *B. crenatus*; it is one which would seem of particular importance for an intertidal form. It is not known how far such temporary 'attachments' become permanent; in the laboratory they do not, but there the surfaces to which the cyprid clings are often widely different from those which it would encounter under natural conditions.

Some observations have been made on the cement by means of which secure attachment to the substratum is attained. It is clear that this takes place in two stages. Primarily, permanent attachment is secured by means of a large mass of cement, produced from the cement glands of the cyprid, which surrounds the bases of the antennae. After metamorphosis, this mass of cement lies approximately at the centre of the basis of the young barnacle and for some time constitutes the sole means of attachment to the substratum, so that the barnacle can be rotated about this central, pillar-like support. Later a thin layer of cement is secreted all over the basis, which then becomes attached to the substratum over the whole of its area.

The staining reactions of the cement, both of that secreted by the cyprid and of that secreted later by the young barnacle suggest, as Yonge (1938) has pointed out, that this secretion is identical with the cuticular layer of the integument. This would suggest that the setting of the cement might take place as a result of a similar series of reactions to those outlined by Pryor (1940). Some preliminary observations were made along these lines in the course of this work, but these need considerable amplification before it can be stated that the setting of the attachment cement is due to the 'tanning' of a muco-protein.

FACTORS INFLUENCING SETTLEMENT

Many workers have investigated the factors which seem to affect barnacle settlement, but it is difficult to find much unanimity of opinion as to the relative importance of the various factors concerned. The range of species covered in these investigations is, however, considerable and, as it is reasonable to suppose that any one factor will not necessarily play as important a part in influencing settlement of one species as it will with another, confusion may have arisen because of the range of species used as experimental material. The following notes apply only to the settlement of *B. balanoides* on structures continuously immersed; contrary to general experience, these studies have shown that this species can settle, metamorphose and grow on such surfaces, though settlement is probably less dense than on intertidal surfaces.

Nature of the Surface. In the course of its 'walking' motion over a surface, a cyprid can cover appreciable distances (Visscher, 1928, records that this type of motion may persist for an hour, during which a distance of the order of 12 mm. can be covered) and it is therefore possible for the larva to encounter a range of surface conditions, some of which may be more suitable for settlement than others. Primarily, settlement is usually confined to cracks, crevices and other irregularities of the surface, though, if the supply of settling stages is maintained, this distinction may later disappear. Pomerat & Weiss (1946) have recently described the extent to which settlement can occur on a wide range of substrata and have found wide variations in the populations of barnacles (*B. improvisus* and *B. amphitrite niveus*) which settled on these surfaces during an exposure period lasting 3 months. The results of exposures of a number of different types of surface during the settlement period for *B. balanoides* in 1944, when cyprid larvae were particularly abundant, are given in Table II.

TABLE II. DENSITY OF SETTLEMENT OF *B. BALANOIDES* ON DIFFERENT SURFACES

Coating applied	Nature of surface produced	Density of settlement No./sq.in.
Anti-corrosive paint (non-toxic)	Smooth; slight surface irregularities	105
Cementiferous protective composition	Granular	77
Rosin-paraffin wax	Waxy	90
Stearic acid	Fatty	68
Petroleum jelly-paraffin wax mixture	Greasy	1
Zinc ricinoleate	Surface completely covered with a heavy, jelly-like slime over period of settlement	1
Aluminium ricinoleate	Surface completely covered with a very heavy, jelly-like slime over period of settlement	1

Though settlement on the non-toxic paint surface proved heavier than that on the other types of surface exposed, settlement occurred to an appreciable extent on all surfaces except those covered with slime and that which had a greasy, unstable finish. The slime which developed on the metallic soap surfaces exposed was far heavier and more viscous than that which often develops on a painted surface, but observations made by Dr M. F. Spooner (personal communication) suggest that the latter type of slime (which is most commonly bacterial in origin) can be as effective in preventing settlement. During a very heavy settlement of the cyprid of *B. balanoides* at Caernarvon in April 1943, she noticed that some of the surfaces exposed had acquired a slime film, which in places was stripping away; settlement of cyprids was wholly confined to those areas thus denuded of slime.

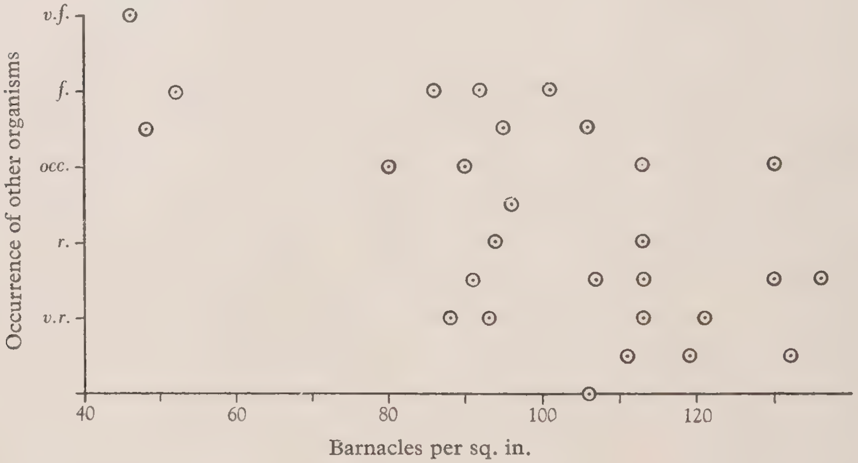

Fig. 3. Effect of the presence of other organisms on the density of settlement of *Balanus balanoides*. The former is classed in eight grades, ranging from 'none' to 'very frequent' (*v.f.*); alternate intermediate grades are denoted 'very rare' (*v.r.*), 'rare' (*r.*), 'occasional' (*occ.*), and 'frequent' (*f.*).

Presence of Other Organisms. Fig. 3 shows the relationship between the density of settlement of *B. balanoides* and the presence of other sedentary forms; in general, the presence of other organisms in any numbers would seem markedly to reduce the density of settlement of this species of barnacle. It should perhaps be added that the other organisms present on these surfaces were *Obelia*, *Ectocarpus* and *Enteromorpha*, since the type of organism present is clearly important; a surface covered with *Mytilus* or with other barnacles will not interfere with settlement to the same extent.

Light and Water Currents. A number of workers (Visscher, 1928; Visscher & Luce, 1928; Neu, 1933), have investigated the effect of light on the settlement of the cyprid larva of a number of barnacle species, and generally seem to have concluded that this larva reacts negatively to light at the time of its attachment and that barnacle settlement takes place most readily on shaded surfaces. The colour of the substratum has also been found to be of importance, settlement of the cyprid taking place most readily on darker colours (Visscher & Luce, 1928). In their study of the effect of surface angle and of light on the attachment of barnacles, Pomerat & Reiner (1942) conclude that the photic factor is of primary importance in the attachment of *Balanus eburneus*. McDougall (1943), however, suggests that the effect of the quantity and quality of the incident light and the tone of the surface of submerged objects, though they influence the settlement of the cyprid, need further investigation before their action can be regarded as definite.

In the course of this work a series of exposures was made which illustrates the difficulty of drawing definite conclusions on the effect of light on settlement. In the spring of 1944 a number of mild steel panels, each 24 in. × 24 in., coated with a non-toxic paint, were exposed to investigate variations in density of settlement over a limited area. The upper edges of the panels lay some 18 in. below the surface and the fifteen panels exposed were distributed at random through the seven exposure bays available on the raft used for this experiment (see Fig. 4). Settlement of the cyprids of *B. balanoides* was heavy during April 1944, and at the end of this period the panels were withdrawn and the density of settlement estimated, for each panel, by counting the numbers of barnacles present with 2 in. × 2 in. areas chosen at random from each square foot of each face of each plate. Eight areas were thus counted for each panel. The mean density (as individuals/sq.in.) for each face of each plate is given in Fig. 4.

The exposure conditions of the panels situated at the end positions in each bay differed from those situated towards the centre of the bays in that the face towards the outside of the raft (i.e. those towards the nearest end of each bay) was shaded by the presence of a buoyancy drum lying immediately outside it. Inspection of the density of settlement on these faces shows that it was always higher than on the inner, better lit face. This suggests heavier settlement on the shaded surfaces; but an inspection of the density of settlement on the more centrally-situated panels shows similar—or even greater—differences between the two faces of most of them. The lighting of the two faces of these panels was certainly more equal than it was for panels exposed at the ends of the bays and therefore, if light were the most important factor concerned, a greater similarity in density of settlement should have occurred.

Walton Smith (1946) has recently drawn attention to the effect of water currents on the settlement of barnacles and his experiments have shown that permanent settlement of the cyprid can be prevented by currents of the order of 1 knot or less. This factor may clearly also play a part in controlling density of settlement. In the experiments under discussion, those panels at the ends of the bays are not only shaded on their outer faces, but these faces may possibly also, because of the buoyancy drums outside them, be in 'dead' water for slightly longer periods in each tidal cycle. The limiting current speed for *B. balanoides* is not known, but it would seem possible to suppose that this was exceeded for slightly shorter periods per tidal cycle for the outer faces of these panels than for their inner faces and, given the presence of a considerable number of settling larvae, this might therefore lead to heavier settlement on the outer faces.

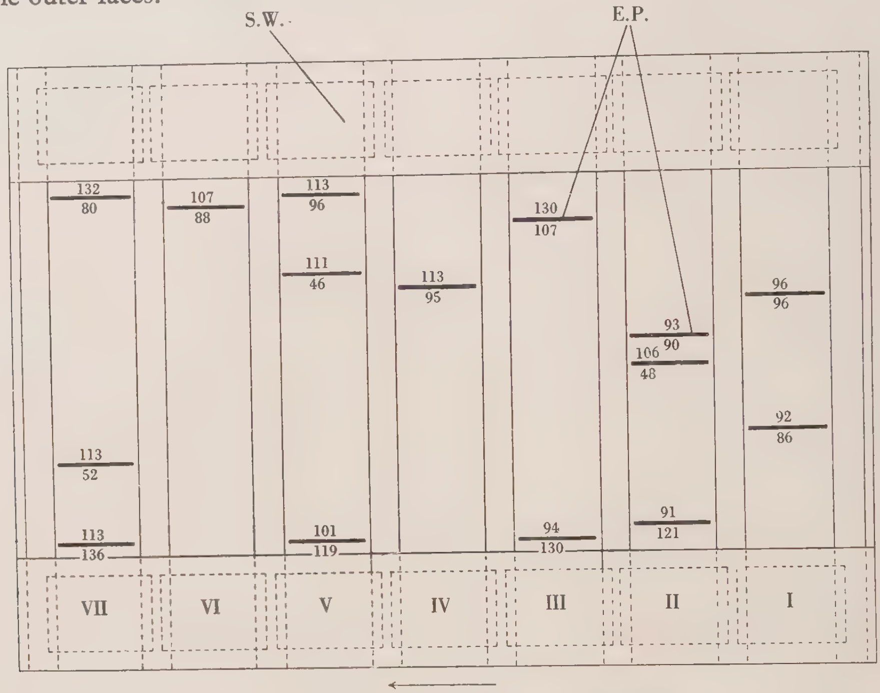

Fig. 4. Plan of raft, showing positions of exposures for observations on the density of settlement of *Balanus balanoides*. The roman numerals indicate the numbers of the exposure bays. The arabic figures, set against each side of the exposure panels (E.P.), represent density of barnacles, as explained in the text. S.W., side-walk with the buoyancy drums beneath. The arrow at the foot of the plan represents direction of the ebb tidal flow. The raft is moored with its ends facing NNE. (bay I) and SSW. (bay VII).

The possibility that current speeds play some part in influencing density of settlement also means that the occurrence of differences in density of settlement on the two faces of panels immersed towards the middle of these bays is less anomalous than if light were the sole controlling factor. This raft is moored so that its long axis lies approximately parallel with the tidal current but the panels suspended from it are not orientated accurately edge on to this current, hence it is possible that this, coupled with the effects of neighbouring panels, might lead to differences in the period of slack water per tidal cycle on the two faces of the panels, and so to differences in density of settlement. Other exposures suggest that marked differences in water flow may be present.

At the site where this exposure raft is moored, the ebb tide (indicated by an arrow on Fig. 4) is far stronger than the flow. If this suggestion of the effect of water currents is correct, therefore, those panels situated towards the middle of the end bay on the 'ebb end' of the raft should, because of the absence of interference from either buoyancy drums or other panels, be likely to show the most similar conditions on their two faces. It is therefore interesting to find that the population densities on the two faces of the panels immersed in this position (i.e. towards the centre of bay 1, see Fig. 4), are virtually identical.

It is clear that this hypothesis that current speeds play at least as important a part in affecting settlement as light can only be advanced tentatively, but laboratory evidence does not indicate that the cyprid of *B. balanoides* reacts negatively to light at the time of attachment. If these larvae are kept in a tank lit from one side, they cluster thickly on the lighted face. Settlement usually begins elsewhere in the tank, but later, when death and settlement have reduced the numbers of free-swimming larvae swarming over the lighted face, settlement takes place readily there, which suggests that lack of settlement over this face initially was due to the mechanical interference of large numbers of free-swimming forms. If the numbers of cyprids are reduced so that crowding on the lighted face is not excessive, settlement starts on that face.

Mention has been made earlier in this section of the effect of colour of substratum on settlement. This survey has provided little additional evidence, which can be regarded as at all conclusive, on this point. Though exposures of non-toxic paint surfaces of different colours, made in 1944, did not indicate any marked differences in density of settlement on the various colours employed, conditions of exposure were not critical enough to allow much importance to be attached to this result.

METAMORPHOSIS

Observations on shore settlements indicate that metamorphosis takes up to 48 hr. to be completed; these observations also emphasize the heavy mortality which occurs during this process, as roughly 50% of the original population observed died during metamorphosis.

DENSITY OF SETTLEMENT

In the course of other experiments, a number of observations have been made on the density of settlement at various stages. The most relevant observations are given in Table III.

TABLE III. POPULATION DENSITIES OF *B. BALANOIDES* AT DIFFERENT STAGES

Stage	Number/sq.in.	Date and place of record
Newly settled cyprids	480	Millport, April 1945
Young barnacles	106	Millport, April 1944
Young barnacles	76	Millport, April 1945
Barnacles, over 2 months old	65	Carnarvon, July 1943

These observations emphasize the heavy mortality which occurs after settlement, but it should be added that the difference between the newly settled cyprid and the young barnacle populations has possibly been over-emphasized, as the former count was made from an intertidal area and may thus include some larvae present on the surface due to the 'clinging' reaction mentioned earlier and which may not have been permanently attached. The density of the 2-month-old population is high compared with that of many intertidal areas, but all the individuals were extremely elongated and resembled the specimens of *B. balanoides* var. *elongatus* Gould. mentioned by Moore (1935*b*).

THE ADULT BARNACLE

It is interesting to find that *B. balanoides*, so typically an intertidal form, can settle and metamorphose in some numbers under conditions of continuous immersion. Settlement under these conditions, moreover, is not confined to the region immediately below the water, as an exposure made in 1944 showed that settlement of *B. balanoides* could take place down to a depth of over 5 ft. below the water-line. Other records are available (Mr R. Elmhirst, personal communication) of the settlement of *B. balanoides* below low-water mark, e.g. it has been found, though not in large numbers, on *Laminaria*. No detailed observations have been made on the growth rate of individuals continuously immersed but it was evident to the eye that growth, at any rate over the period immediately following settlement, was more rapid in continuously immersed individuals than in forms which had settled on the shore. As opportunities for feeding are not limited for the individual below the water-line in the way they are for an intertidal specimen, this might be expected. It would be of interest to know more about the general biology of such individuals, since continuous immersion modifies a number of the factors of the normal habitat of this species. For example, such individuals are not subject to the high temperatures which can occur on the shore during the summer and therefore the curious intermittent growth, described by Hatton & Fischer-Piette (1932), might not occur.

BALANUS CRENATUS

DEVELOPMENT OF LARVAE AND THEIR OCCURRENCE IN THE PLANKTON

The breeding habits of *B. crenatus* differ markedly from those of *B. balanoides* for, whereas the latter liberates larvae only over a limited period of the year, *B. crenatus* liberates larvae at intervals from early spring onwards through the summer.

Fig. 5 shows the results of a series of examinations of small populations of this species, similar to those made for *B. balanoides*, over a period extending from mid-January to the beginning of May. Four arbitrary stages could be recognized in the development of the larvae, based upon the colour of the ovigerous lamellae. In the 1st stage the ovigerous lamellae were white in colour and creamy in consistency; microscopic examination showed them to contain unsegmented ova. In the 2nd stage the white colour persisted, but each lamella now formed a discrete mass within the mantle cavity; the ova were beginning to segment. In the 3rd and 4th stages, the ovigerous lamellae became coloured; but at first they became much more transparent in appearance and pink or light brown in colour (stage 3), the colour later darkening to a deep purple (stage 4). In stage 3, the outlines of the larva are clearly visible within each vitelline membrane and the rudiments of the appendages could be detected; in ova from 4th stage ovigerous lamellae the larva was fully formed and the median eye spot visible.

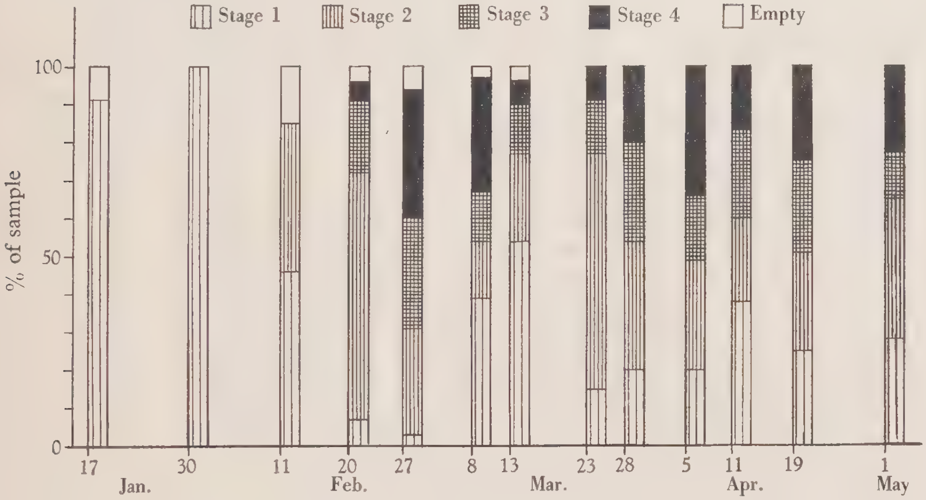

Fig. 5. *Balanus crenatus*. State of development of ova, 1946.

A comparison of Fig. 5 and Fig. 1 suggests that development of the ova started later in *B. crenatus* than in *B. balanoides* but, once started, progressed more rapidly as populations of both species showed a small proportion of individuals containing larvae ready to hatch at about the same time. From then onwards some proportion of the barnacles examined contained larvae ready to hatch. Examinations of samples of *B. crenatus* were continued for the rest of the year and individuals containing larvae ready to hatch were last recorded in a sample collected on 30 August. The maximum percentage of individuals containing larvae ready to hatch, however, fell steadily through the summer, in February 34% was the maximum recorded, in March 30%, in April 34%, May 20%, June 18%, July 8% and in August 6%. This suggests that over each period of liberation, the numbers of larvae liberated decreased and therefore the numbers of cyprids available for settlement should grow steadily less: fig. 8 confirms this.

Fig. 6 presents the analysis of counts of *B. crenatus* larvae for 1947 over the period of the year when they are most abundant—March and April.[1] 1st and 2nd stage nauplii (which have again been grouped together because the 1st stage moults to give the 2nd stage within a few hours of liberation) first appeared in any numbers during the 3-day period beginning 20 February. In 1946 they first appeared in number on 27 February, in 1945 on 4 March and in 1944 on 24 February, so that their appearance in the plankton in 1947 was earlier than in the preceding 3 years. The factors which govern the date on which the early larvae become common in plankton hauls are not known, but there is no direct relationship with water temperature.

3rd stage nauplii first appeared on 4 March; 4th stage nauplii on 7 March, 5th stage nauplii on 13 March, 6th stage nauplii on 16 March, and the first cyprids were recorded on 22 March. This suggests that again roughly 30 days are required between hatching and the appearance of the cyprid larva. This estimate may be compared with the sequence of events in a laboratory culture which was successfully reared through the complete larval sequence in July and August 1942 (Table IV).

TABLE IV. RATE OF DEVELOPMENT OF *B. CRENATUS* IN THE LABORATORY

Larval stage	Time of appearance (days after hatching)
Nauplius I	—
Nauplius II	1
Nauplius III	8
Nauplius IV	11
Nauplius V	13
Nauplius VI	?15
Cyprid	16

This laboratory record compares reasonably well with the estimated period taken from hatching to the appearance of the cyprid in the sea, when it is remembered that development in the laboratory was carried through at a temperature of 15° C. or more, and the sea temperatures prevailing during February and March 1947 were 4–5° C.

Herz (1933), in his account of the larval stages of *B. crenatus*, described eight naupliar stages. In the course of the present work it has not been possible to discover more than six naupliar stages, of which a detailed description will be given in a later paper. Bassindale (1936) has discussed the validity of the 2nd stage nauplius described by Herz. It would seem unlikely that two species of *Balanus* should differ in the number of their naupliar stages, when there are no differences of this nature between species belonging to different genera, as *B. balanoides*, *Verruca stroemia* and *Chthamalus stellatus* each have six naupliar stages (Bassindale, 1936). It is possible, however, that the number

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[1] As an indication of the numbers of larvae taken, the following are the average daily hauls, over the period shown in Fig. 6, for each larval stage: Nauplius I+II, 695; Nauplius III, 545; Nauplius IV, 1195; Nauplius V, 1560; Nauplius VI, 955; Cyprid, 970.

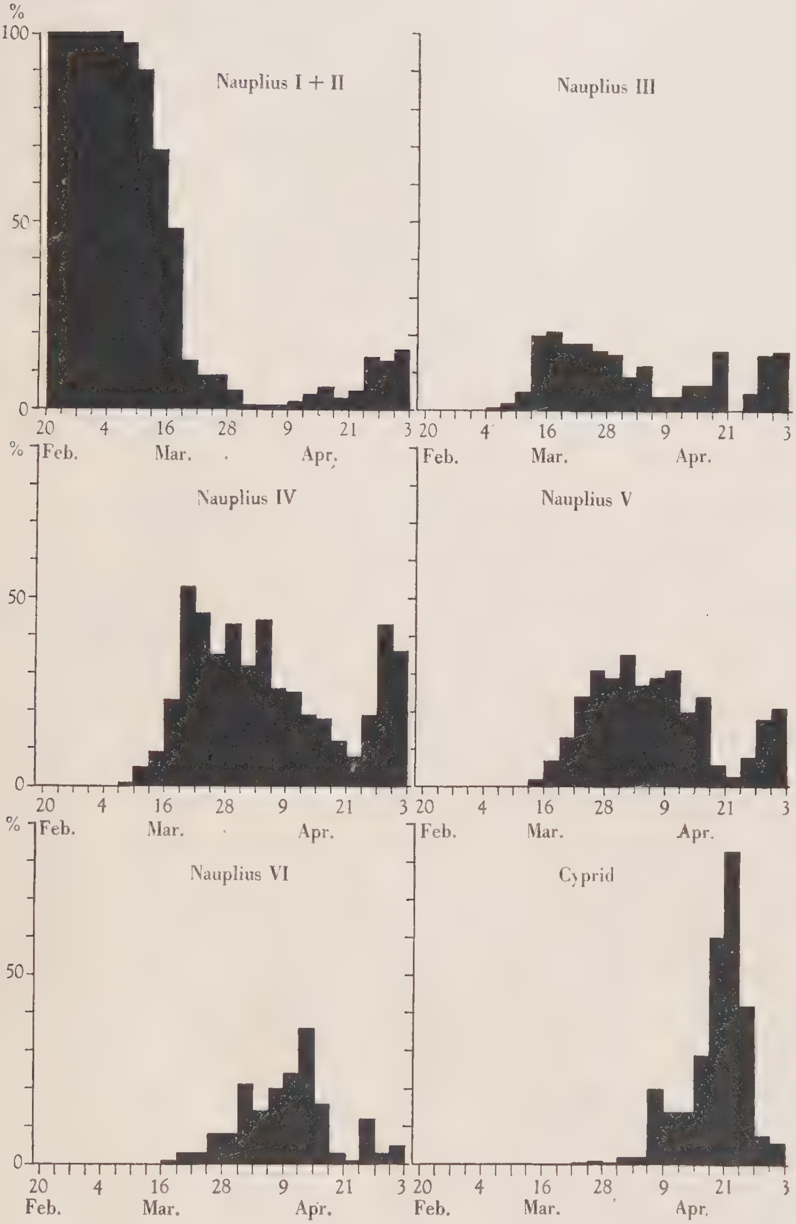

Fig. 6. Occurrence of the larval stages of *Balanus crenatus*, spring 1947. The numbers present, over 3-day periods, of each larval stage are expressed as a percentage of the total *B. crenatus* larvae present.

of naupliar stages may vary for the same species. Macdonald (1927), for example, has described irregularities in the larval sequence of *Meganyctiphanes norvegica*, and comparable differences might occur in the larval sequence of *Balanus crenatus* from different places.

It is evident from Fig. 6 that the proportions of 3rd stage *B. crenatus* nauplii and of later larval stages did not provide the sequence of maxima which characterized the corresponding stages of *B. balanoides* (cf. Fig. 2), and consequently further analysis cannot profitably be made. Further, since the histograms shown in Fig. 6 represent proportions rather than direct counts some of the characteristics of the occurrence of the larvae of *B. crenatus* in the plankton at this period are obscured, in particular, the occurrence of especially heavy hauls early in April. Fig. 7, which shows the actual numbers of larvae recorded (from the 3rd naupliar stage onwards), for both *B. crenatus* and *B. balanoides*, plotted as 3-day averages, indicates the preponderance of *B. crenatus* larvae up to the period beginning 6 April and the larger numbers of *B. balanoides* larvae which were present thereafter. This preponderance of *B. crenatus* larvae early in April is, on the basis of the restricted evidence provided by this limited survey, not usual and was probably caused by the failure of the earlier-hatched *B. balanoides* larvae.

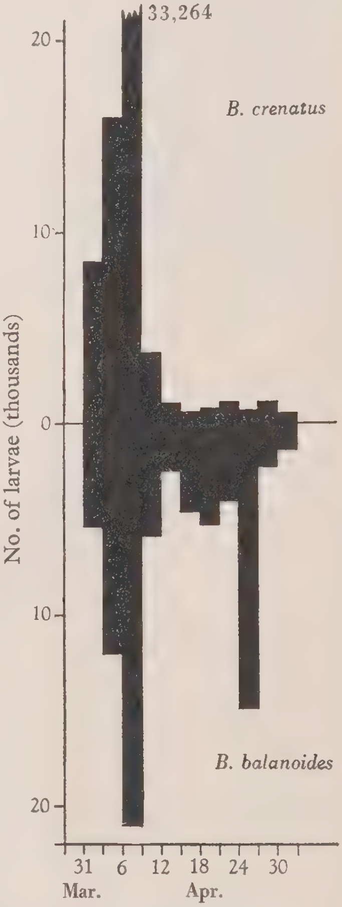

Fig. 7. Numbers of *Balanus crenatus* and *B. balanoides* larvae present in the plankton during April 1947 (shown as 3-day averages).

Comparisons of the numbers of cyprid larvae of *B. balanoides* and *B. crenatus* present in a series of plankton hauls must be made tentatively and in this instance with particular caution since, as has already been mentioned, the hauls on which these statements are based were made only at one period during the tidal cycle. There is some suggestion, in the records accumulated in this survey, that *B. crenatus* cyprids become more abundant later in the tide, i.e. as the ebb falls away to slack water. It is hoped to investigate this point more fully later but if the point is then substantiated, it is evident that the results just discussed may be erroneous in the emphasis laid on the abundance of the cyprids of *B. balanoides*. This point raises the whole question of the possibility of a relationship between larval abundance and the time in the tidal cycle at which hauls were made. Some observations have been made which indicate that such variations do occur, but a fuller investigation, on a more strictly quantitative basis, is needed before the problem can be discussed further.

Earlier in this paper, an attempt was made to estimate the success of larval development of *B. balanoides* by comparing the numbers of cyprids and the numbers of 1st and 2nd stage nauplii. On this basis the February–March liberation of *B. crenatus* nauplii can be counted as successful, as the cyprids recorded early in April represent nearly 70% of the nauplii hatched at the end of February and early in March.

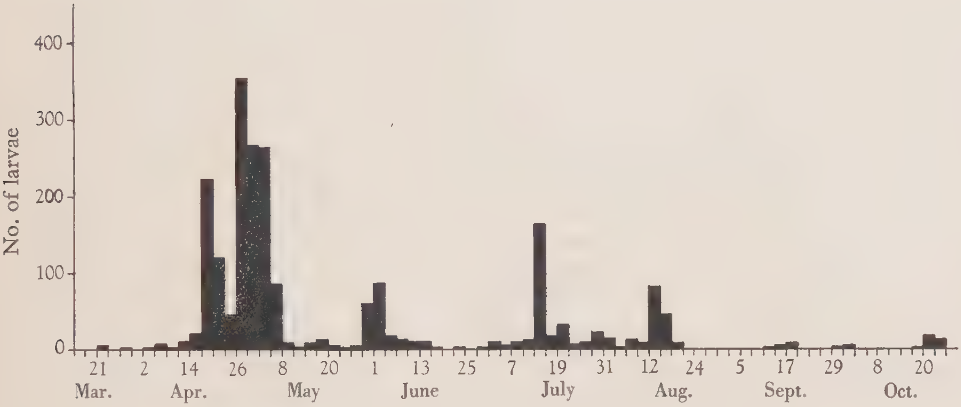

Fig. 8. Occurrence of cyprid larvae of *Balanus crenatus*, 1946. Numbers of larvae per haul in 3-day averages.

Examination of hauls later in the year shows that the larvae of *B. crenatus*, particularly the later-stage nauplii and the cyprids, are most common at intervals through the summer. Fig. 8 shows the recorded occurrence of the cyprids of *B. crenatus* from mid-March to the end of October 1946. Maxima occurred during April (and especially at the end of that month), at the end of May and in the middle of July and August. As these records are based on hauls made from Keppel Pier, these variations might have been caused by variation in tidal strength between springs and neaps[1], but as records for the settlement of this species show that this also was periodic, it would seem likely that these plankton records present a true picture of the situation. This periodicity in the reproduction and settlement of *B. crenatus* does not seem to have been recorded before, but it gives rise to marked differences in size between individuals which have settled, some early and some later in the season. On occasion, the assumption that *B. crenatus*, like *B. balanoides*, settles only at one period of the year has led to misinterpretations. For example, Foxon (1940) bases statements on the period for which the externa of *Sacculina carcini* had been in place on the occurrence of specimens of *Balanus crenatus* of two sizes on the carapace of the host. The crabs were collected in August, so it would seem quite possible that all the *B. crenatus* present had settled during the spring and summer of the same year, and did not, as Foxon supposes, belong to settlements of two successive years.

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[1] Spring tidal periods were: 3–6, 19–20 Feb.; 5–8, 19–22 Mar.; 5, 18 Apr.; 3, 15–18, 31 May; 13, 28 June; 12, 27 July; 11, 25 Aug.; 13–15, 24 Sept.; 13–15, 27 Oct., 1946 and 9, 22–26 Feb.; 10–12, 25 Mar.; 8, 23 Apr., 1947.

SETTLEMENT

On the basis of laboratory observations, the cyprids of *B. crenatus* settle much more readily than those of *B. balanoides* for, whereas the latter usually do not settle until some 5 days after catching, the cyprids of *B. crenatus* are settling in some numbers less than 48 hr. after collection and settlement may be virtually complete after 72 hr. Probably this does not represent a physiological difference between the two species, but rather is an expression of the fact that conditions of continuous immersion in a tank of sea water are less abnormal for *B. crenatus* than they are for the larvae of *B. balanoides*. It is of interest again to note that the cyprids of *B. crenatus* retain their positive reaction to light up to the time of settlement; the latter process takes place most abundantly over the best-lit areas of the storage tank.

As the settlement period of *B. crenatus* is so much longer than that of *B. balanoides*, colonization of an exposed surface is rarely so intense and opportunities have not occurred, therefore, to make observations on the conditions affecting settlement of *B. crenatus* comparable with those made for *B. balanoides*, though no indications have been noticed which would suggest that the reactions of the cyprid of *B. crenatus* to slimy or fouled surfaces differ markedly from those of the cyprid of *B. balanoides*.

As might be expected for a species with a normal vertical range lying mainly below low-water mark, *B. crenatus* settles in greater abundance at some distance below the water-line. Table V gives the density of settlement at various depths on a surface exposed from late June to late August 1945 which is typical of the vertical distribution of this species. In confirmation of the periodicity of settlement, this population was also distinctly bi-modal,

TABLE V. VERTICAL DISTRIBUTION OF *B. CRENATUS*

Depth below water-line (ft.)	Nos. (barnacles per sq.ft.)
0·5–1·5	1
1·5–2·5	10
2·5–3·5	8·5
3·5–4·5	32
4·5–5·5	62·5
5·5–6·5	120·5
6·5–7·5	128
7·5–8·5	100·5

consisting of a recent settlement—probably early August—and an earlier settlement, probably early July.

From this table it is evident that settlement has been heavier some distance below the water-line; 75% of the settlement was limited to depths greater than 5 ft. It should, however, be emphasized that these data have been obtained from a floating object, since the surface was immersed from a raft.

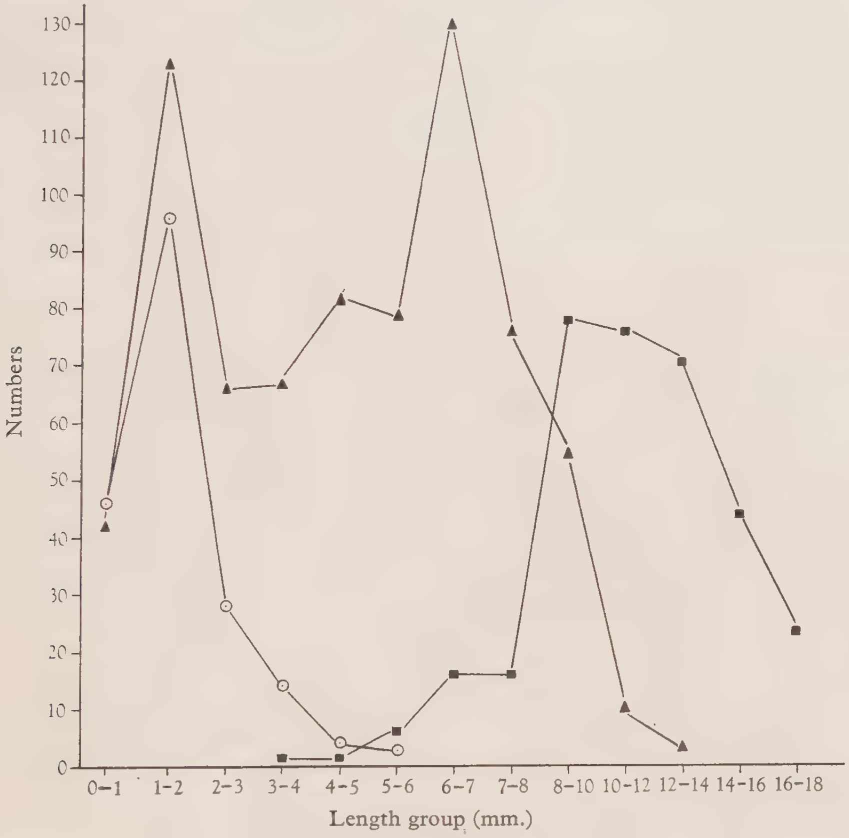

Fig. 9. Analyses of populations of *Balanus crenatus*, 1943.
—⊙— 26 June; —▲— 24 July; —■— 14 Sept.

The characteristic feature of the settlement of *B. crenatus* is its periodicity. Fig. 9 gives records of the measurements made on a population of *B. crenatus* which settled on a surface first exposed towards the end of May 1943. 32 days later 191 *B. crenatus* had settled on one face (4 sq.ft.), their modal length group (1–2 mm.) indicating that settlement had occurred shortly before the surface was examined. Roughly 2 months after immersion the population had risen to 735 over the same face and the length-group distribution was distinctly bi-modal; one mode occurring again in the 1–2 mm. basal length group (and therefore representing a recent settlement) and the other (presumably representing the June settlement) in the 6–7 mm. group. Just over 2 months later, the surface was again examined and the population again proved to be uni-modal, with a rather ill-defined mode in the 8–10 mm. group. This single mode could have been produced by the merging of the two settlements so evident at the earlier inspection if it is assumed that the growth curve of a single individual follows the usual sigmoid form. The total population present, however, was only about 50% of that present at the previous inspection and this reduction in numbers, which seemed to have been due to the colonization of the surface by other organisms, which smothered and killed part of the barnacle population, may well have obscured the true relationship of the two settlements at this last examination. Prior colonization of the surface may also have eliminated the possibility of a settlement during August. Comparable observations, clearly indicating periodicity of settlement, have also been obtained (in 1946) for exposures covering April and May.

Growth Rate and Maturity

These observations on periodicity of settlement also provide a means of estimating the growth rate of this species. The results are given in Table VI and are shown graphically in Fig. 10. In all cases the length of the basis was measured. Moore (1934) has advanced reasons for preferring measurements which allow the volume of the shell to be estimated; this estimation is clearly preferable and indeed essential if the populations measured are growing under crowded conditions. In the present instance, however, each individual had ample room to grow unrestricted by its neighbours, so that basis measurements are likely to give a reasonably reliable estimate of growth rate.

Table VI. Growth Rate of *B. crenatus*

Date of examination	Approx. interval since settlement (days)	Modal length group (mm.)	Mean increase in length per day (mm.)	Maximum length group (mm.)
30. iv. 46	5	0–1	—	—
5. vi. 46	40	5–6	0·14	—
2. vii. 46	67	10–12	0·20	14–16
26. vi. 43	10	1–2	0·15	—
24. vii. 43	39	6–7	0·17	—
14. ix. 43	91	10–12	0·12	20–22
25. x. 46	?40	5–6	0·14	—
17. xii. 46	?93	6–7	0·02	—
25. i. 47	?132	6–7	0	—
27. ii. 47	?165	6–7	0	8–10
19. v. 47	?246	10–12	0·06	—
19. vi. 47	?277	14–16	0·13	18–20

Growth evidently takes place steadily through the summer months, but is arrested during the winter. There is no suggestion, for this species, of the

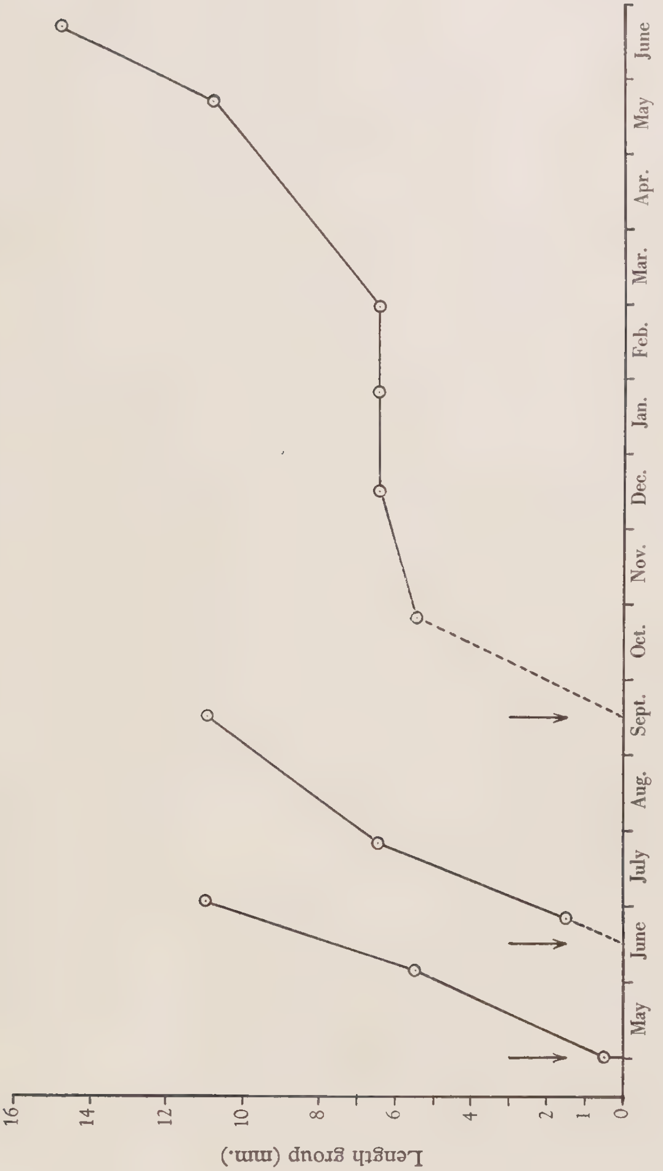

Fig. 10. Growth rate of *Balanus crenatus*. The arrows indicate the approximate date of settlement.

limitation of growth to a short period early in the summer, as has been recorded by Hatton & Fischer-Piette (1932) for *B. balanoides*. There is also little sign of any direct correlation with water temperature, for example, during the period between the end of April and the beginning of June 1946, when growth was taking place at a mean rate of 0·14 mm./day, the mean sea temperature was 8·4° C., whereas later in the year, between the end of October and the middle of December, when growth had practically stopped (a mean increment of only 0·02 mm./day) the mean temperature was 9·6° C. Food supply would seem a more likely limiting factor.

Topsent (1911) has given records of the growth rate of *B. crenatus* on the shore; under these conditions *B. crenatus* grows much more slowly, as the basis had achieved a length of only 5–6 mm. some 3½ months after settlement.

The last set of observations in Table VI, which cover autumn and winter growth rates, have also provided a little information on winter mortality. By mid-December 8% of the original population were dead and by the end of January the death rate had risen to 19%. Thereafter mortality was slight, as the death rate at the end of February was 20% and that in mid-May 21% of the original population. The original settlement was light (density 230 barnacles/sq.ft.) so that it is unlikely that many, if any, individuals were 'crowded out'. The incidence of heaviest mortality in the period October–January suggests the elimination alike of such adverse factors as decrease in water temperature—this was much lower after January, the rate of temperature decrease being much the same over the pre-December and the post-December periods (a decrease in the mean monthly temperature of 3·4° C. for the former and 3·1° C. for the latter)—and the settlement of other fouling forms. Some of the larger brown algae may settle before the end of January (e.g. *Laminaria*, *Saccorhiza*, *Desmarestia*), but their growth is negligible until much later in the year. Food supply might therefore be the factor most likely to affect the population adversely at this time.

These growth-rate estimates, since they are based on modal length groups of populations, express the modal growth rate only. As is shown by the figures given in the last column of Table VI, these can be far exceeded by a few individuals in the population and it would seem, from the second set of measurements recorded, that *B. crenatus* can reach a basal length of just under 1 in. in 3–4 months after settlement. Darwin (1854) states that the largest specimens of *B. crenatus* he had seen measured 0·55 in. (roughly 14 mm.) in basal diameter; measurements of the basal length (which closely approximates to basal diameter for this species growing unrestrictedly) of a large number of individual *B. crenatus* made during the present survey indicate that the largest specimens came within the 28–30 mm. length group. As has just been mentioned, 3–4 months' growth can produce a barnacle with a base 20–22 mm. in length and this series of observations has also shown that, given a slightly longer growing period, a basal length of 26–28 mm. can be attained in the year of settlement. A specimen of *B. crenatus* which settles early in April can therefore virtually reach the maximum recorded basal length before the end of the growing period of its year of settlement.

When the first set of growth-rate observations recorded in Table VI were discontinued early in July, the population was examined and the state of development of the ovigerous lamellae determined. The results are shown in Fig. 11. Some proportion of all the individuals of basal length greater than 4–5 mm. showed the presence of developing ova in the ovigerous lamellae, and individuals of basal length 12–14 mm. or more all contained developing ova. Most of these ova were in the early stages of development (Stages 1 or 2, see p. 477) but one individual, of 12–14 mm. basal length, contained larvae ready to hatch. *B. crenatus* evidently attains maturity a very short time after settlement, as individuals which had settled late in April presumably could themselves liberate larvae during July.

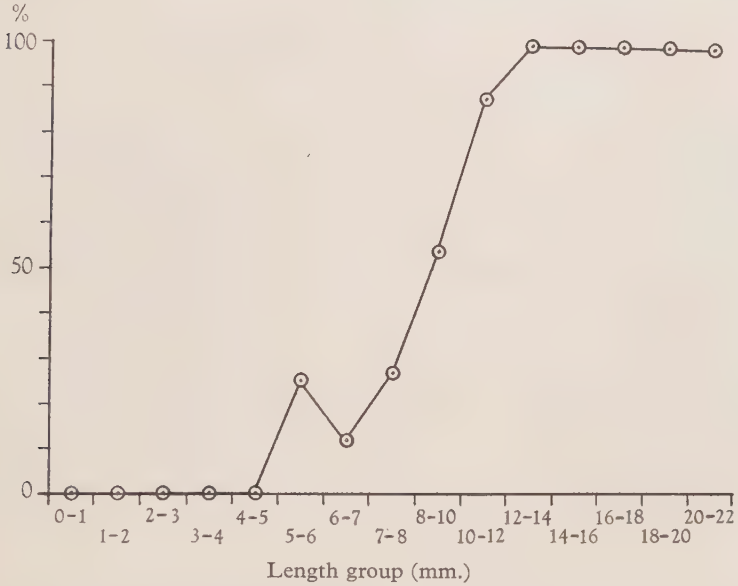

Fig. 11. Occurrence of developing ova in young *Balanus crenatus*, expressed as percentage of individuals containing them.

Individuals which settle in the autumn are mature, as perhaps might be expected from the foregoing observation, the following spring. For example, a proportion (roughly 30%) of the population which settled in the autumn of 1946 (see Table VI) was examined in May 1947. 77% of these individuals contained developing ova at some stage, and of those in this condition roughly half contained larvae ready to hatch.

Moore (1934) finds that most of the 'lower- and middle-zone (*B. balanoides*) die in their 3rd year, but those from the top zone may live for 5 years or more'. Exact data of the length of life of *B. crenatus* are not available, but the impression gained is that the latter species has a shorter life than even the 'lower- and middle-zone' *B. balanoides*; it seems possible that a *B. crenatus* which settles in the spring, may die in the autumn of the following year. Present evidence suggests that it spawns twice and possibly three times during this period, once later in the summer of the year of settlement, once the following spring and possibly once again later that year.

VERRUCA STROEMIA

Occurrence of Larvae in the Plankton

Observations on this species have been limited to the occurrence of the larvae in the plankton; no data are available on settlement or on the adult barnacle.

The larvae of this species, particularly the 1st and 2nd stage nauplii, rank with the larvae of *Balanus balanoides* and *B. crenatus* as common components of the Cirripede content of the plankton at Millport. The early nauplii of *Verruca stroemia* are present in the plankton for most of the year, e.g. in a detailed survey made from January 1946 to May 1947, these larvae lacked a record only during November, but they are most numerous in the spring and early summer and thus play a significant part in the swarms of barnacle larvae which are so characteristic a feature of plankton hauls made during February, March and April. They are also usually the first to appear in any numbers in plankton hauls made early in the year, e.g. in 1944 they were present on 3 February and in 1945 and 1946 they first appeared on 2 February. By the middle of February, heavy hauls of the 1st and 2nd stage nauplii of this species can often be made. Yet, judged on the basis of plankton hauls made a few feet below the surface, these large numbers of 1st and 2nd stage nauplii which appear early in the year are not immediately followed by the appearance of later nauplii or cyprids, as with *Balanus balanoides* and *B. crenatus*. Fig. 12, which shows the proportion of (*a*) the 1st and 2nd stage nauplii and (*b*) nauplii from the 3rd stage onwards (plotted as 3-day averages) which occurred during the early months of 1947, emphasizes this point. From 20 February until 16 March the only stages present were the 1st and 2nd stage nauplii, the later naupliar stages (3rd stage onwards) did not assume any considerable proportions until 6 April, and cyprids did not appear until the period beginning 30 April.

Further, the period between 20 February and 16 March was characterized by a preponderance of 1st stage larvae—during this period nearly 46,000 1st stage nauplii were recorded, but only just over 9000 2nd stage nauplii. Nilsson-Cantell (1921) found at Bohuslän, W. Sweden, that the 1st naupliar stage occupied about a week, and this prolonged preponderance of 1st stage nauplii in the Clyde plankton suggests that this stage has a longer life period than that of the corresponding stages of *B. balanoides* and *B. crenatus*. In the laboratory, however, the 1st stage nauplius of *Verruca stroemia* moults to give the 2nd stage within a few hours of hatching.

The general sequence of events just described for 1947 also characterized the planktonic occurrence of the larvae of this species for the other years over which this survey extended. Fig. 13 shows the results obtained in 1946. Again, heavy hauls of early larvae were taken early in the year (with a preponderance of 1st stage nauplii, though not quite so marked as in 1947), no heavy hauls of late stage nauplii were made until much later and no cyprids were recorded until towards the end of April.

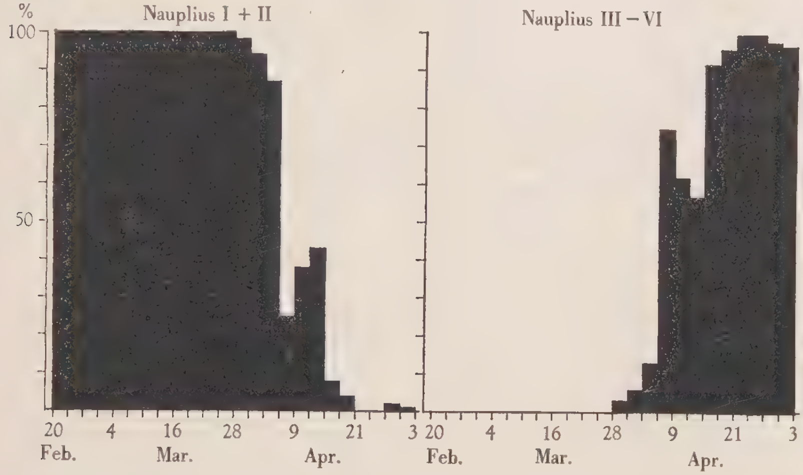

Fig. 12. Occurrence of the larval stages of *Verruca stroemia*, spring 1947. The numbers present, over 3-day periods, of each group of larval stages are expressed as a percentage of the total *V. stroemia* larvae present. (Cyprids were absent except for 2% during the very last period.)

In the absence of settlement data for *Verruca*, any suggested explanation of this situation must remain tentative, but there seem two outstanding possibilities. First, it is possible that only the earlier stages of naupliar development occur near the surface, the later-stage nauplii and the cyprids occurring in any numbers only in deeper water, so that the surface records for these stages are misleading. Secondly, it is possible that the record presented by these hauls is substantially correct and that the sequence of larval stages of *V. stroemia* extends over a period which is much longer than that of the two species of *Balanus* discussed earlier. If the first possibility is correct, it is difficult to see why the periods of abundance of early- and later-stage nauplii should approximate more closely later in the season, whereas if the second possibility is

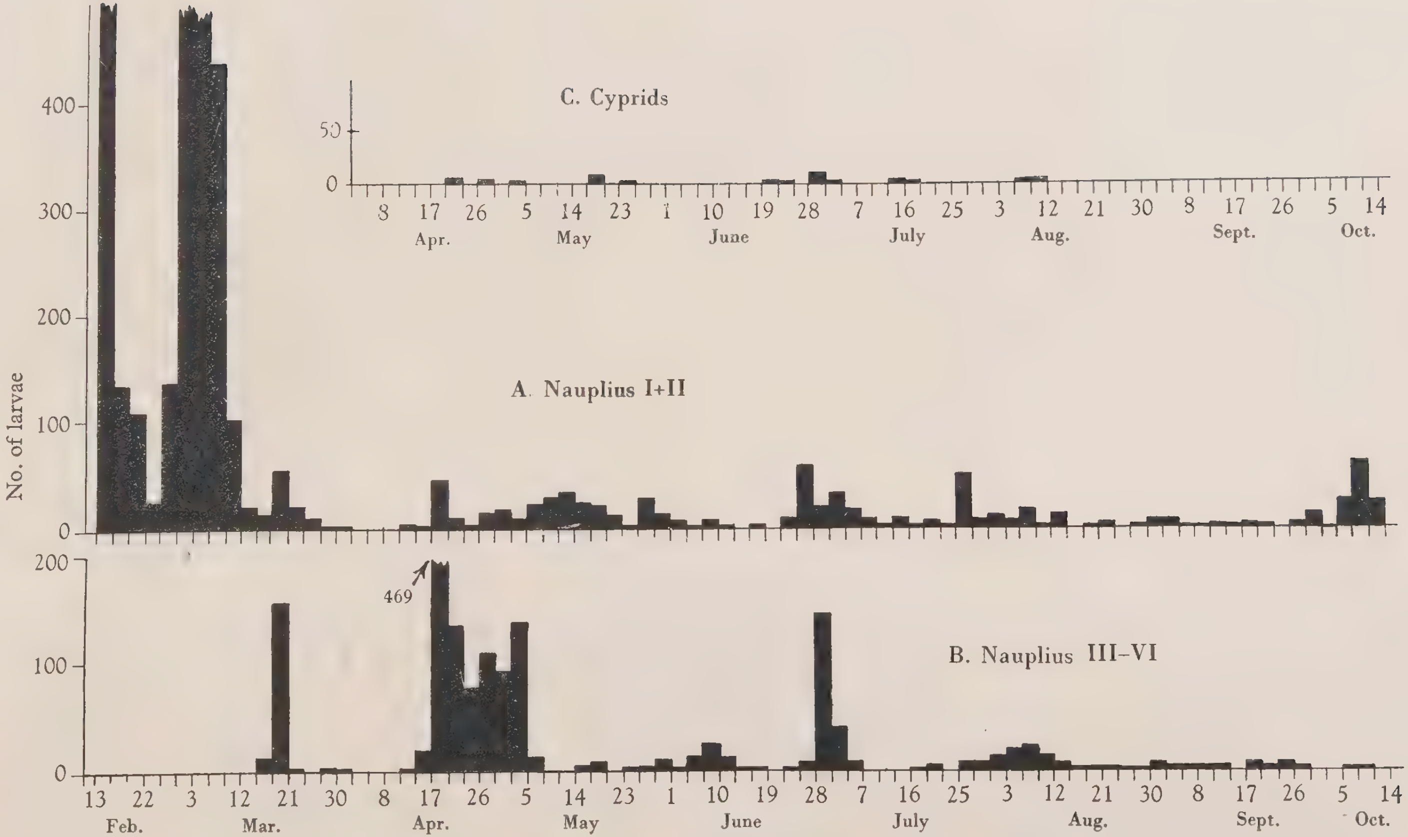

Fig. 13. Occurrence of the larval stages of *Verruca stroemia*, 1946, expressed as the number of larvae per haul, in 3-day averages. A, nauplii I and II. B, nauplii III–VI. C, cyprids.

correct a closer correspondence between periods of abundance later in the year might be expected, as rising water temperatures would presumably accelerate larval development. If the larval sequence does take place slowly early in the season, the early-stage larval maximum (Fig. 13 A) beginning on 13 February could be correlated with the later-stage maximum on 18 March (Fig. 13 B) and possibly with the cyprids recorded around 20 April (Fig. 13 C); the early-stage maximum on 28 February with the later-stage maximum beginning on 17 April and the cyprids occurring in the following month, suggesting that the full larval sequence, from hatching to the appearance of the cyprid, takes roughly 2 months at this season. Such links can only be tentatively suggested, particularly as the cyprid stages are never at all common. There are times during the spring and summer when the later-stage nauplii of *Verruca* are reasonably common (e.g. over 2000 occurred in one haul, made on 30 April 1947) but they do not seem to be followed by comparable hauls of the cyprid larva. Perhaps the latter only occurs in numbers in deeper water and, though slow development may be the explanation of the lack of immediate correspondence between the early- and later-stage nauplii of *Verruca*, surface hauls are not a reliable indication of the abundance of the cyprid larvae.

Though nothing is known of the settlement of this species, it can be predicted, from what is known of the occurrence of the nauplii, that it extends at least over the period April to September and there is a further suggestion that, like that of *Balanus crenatus*, it may be periodic. Fischer-Piette (1932), however, has recorded the appearance of young *Verruca* in abundance on the shore on 7 December and he therefore suggests that the approximate time of settlement lies between September and December. This is rather later than the present observations would suggest.

OTHER CIRRIPEDE LARVAE

The examination of plankton hauls made, for the most part daily, during 1946–47 has afforded an opportunity to assess the abundance of other forms. The only larvae that occurred at all regularly were the nauplii of *Sacculina* (probably *S. carcini*) and those of *Peltogaster paguri*. The *Peltogaster* larvae were at first puzzling, since they differ radically from the figures of the nauplius given by Boschma (1927), notably in possessing a shield-like expansion of the integument, such as Hoek (1909) figures for *P. purpureus*. They agree, however, with the re-description of the nauplius of *P. paguri* given by Reinhard (1946)[1]; and, furthermore, larvae identical with those found in the plankton have been obtained from specimens of *P. paguri* on *Eupagurus bernhardus* collected locally.

The records of these two nauplii are given in Table 7. *Peltogaster* nauplii were present in 10 out of the 14 months covered and it would seem possible that they are liberated all the year round. *Sacculina* larvae, however, proved to be more abundant during the winter months, from November to February or March.

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[1] Dr. Boschma kindly drew my attention to this paper.

TABLE VII. OCCURRENCE OF THE NAUPLII OF *PELTOGASTER* AND *SACCULINA*

Month	Nauplii recorded	
	Peltogaster	*Sacculina*
February (1946)	4	4
March	0	10
April	0	0
May	12	0
June	4	0
July	19	1
August	4	0
September	2	0
October	0	5
November	0	33
December	6	37
January (1947)	8	24
February	29	34
March	10	0

It is of interest to note that these records of the occurrence of *Sacculina* nauplii in the plankton confirm in part the conclusions drawn by Foxon (1940) about the breeding season of this parasite in the Clyde.

DISCUSSION

The descriptions given earlier in this paper of the seasonal occurrence of barnacle larvae in the plankton have clearly indicated their abundance during the months of February, March and April. Tables VIII and IX below set out the average hauls of barnacle larvae per day, for each month of the year, based on the records of this 4-year survey.

In both tables a dash indicates that no hauls were made during that particular month.

The sequence of larvae during the spring outburst is similar year by year. Early-stage nauplii of *Verruca stroemia* and early-stage nauplii of *Balanus crenatus* are the first to appear, usually during the latter part of February and early in March. Early-stage nauplii of *B. balanoides* first appear early in March and reach a maximum towards the middle of that month; the second half of March is characterized by the presence of large numbers of later-stage nauplii of *B. crenatus* and *B. balanoides* sometimes (e.g. in 1946) accompanied by smaller numbers of later-stage nauplii of *Verruca stroemia*. The end of March or the beginning of April sees the appearance of the first cyprid stages and during the first half of the latter month the cyprid of *Balanus balanoides* tends to predominate. During the second half of April the numbers of Cirripede larvae usually decrease and by the end of that month, or early in May, they are reduced to the more modest proportions which they maintain, in general, for the rest of the summer. The numbers recorded after the end of October are negligible. Figs. 14–17 show the details of the records of the nauplii and cyprids of *B. balanoides*, *B. crenatus* and *Verruca stroemia* during the spring outburst in 2 successive years, 1946 and 1947.

Table VIII. All Cirripede Nauplii Month by Month

Expressed as the average number per daily haul

Month	Year			
	1944	1945	1946	1947
January	—	0	0	1
February	1716	21	607	419
March	2846	274	2034	13644
April	515	52	725	12199
May	7	—	136	.
June	—	—	50	.
July	—	—	25	.
August	—	—	21	.
September	—	—	9	.
October	—	—	30	.
November	—	—	0	.
December	—	—	1	.

Table IX. All Cyprid Larvae Month by Month

Expressed as the average number per daily haul

Month	Year			
	1944	1945	1946	1947
January	—	0	0	0
February	0	0	0	0
March	15	5	1	22
April	1491	137	110	2918
May	35	—	68	.
June	—	—	17	.
July	—	—	28	.
August	—	—	17	.
September	—	—	1	.
October	—	—	3	.
November	—	—	0	.
December	—	—	0	.

The figures given in Tables VIII and IX also emphasize the enormous variations that can occur from year to year. For detailed quantitative comparisons, the fishing methods used in this survey were crude, but even so, a difference such as that between the average catch of all stages of all Cirripede nauplii for March 1945 (274 nauplii) and that recorded for the corresponding month 2 years later (13,644 nauplii)—the latter practically fifty times the former—is great enough to be significant. Johnstone, Scott & Chadwick (1924) give figures for *Balanus balanoides* nauplii and cyprids for the period

1907–20, and it is of interest to find that even greater variations appear in their records, e.g. more than two thousand times the number of nauplii were recorded in March 1912 than in March 1907.

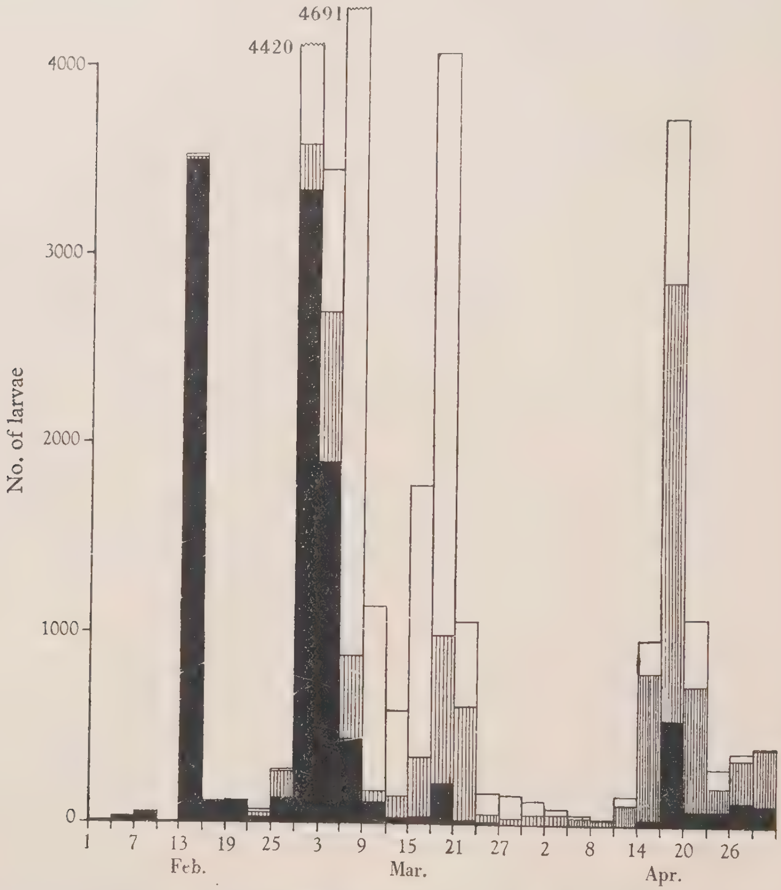

Fig. 14. Occurrence of Cirripede nauplii, Feb.–Apr. 1946. The shaded areas within each histogram indicate the numbers of the larvae of *Verruca stroemia*; the vertically hatched areas the numbers of *Balanus crenatus* larvae; the remaining areas the numbers of *B. balanoides* larvae.

Direct comparisons between the records obtained in the present survey and those obtained by Johnstone, Scott & Chadwick (1924) are impossible since fishing conditions were entirely different in the two surveys. One point, however, seems worthy of mention. Johnstone, Scott & Chadwick (*loc. cit.* p. 66) drew attention to the great discrepancy between the numbers of nauplii and the numbers of cyprids caught, and attributed this to the destruction of the nauplii during their period of development and to the dispersal of the swarms.

The discrepancy recorded for Port Erin is certainly very great (mean monthly haul of nauplii (in March) 35,224; mean monthly haul of cyprids (in May) 70), much greater than that of the present records, where the mean monthly haul of nauplii in March was 140,985 and the mean monthly haul of cyprids in April was 34,920. (The present records refer, of course, to the larvae of all three species of barnacle but, although Johnstone, Scott & Chadwick's account refers to their larvae as those of *B. balanoides*, their specific identity was merely inferred from the abundance of this species on the neighbouring shores; it would seem probable that larvae of other species of barnacle were present.) The present series of hauls were all made within a few feet of the shore and perhaps this may be the reason for the smaller discrepancy between the numbers of nauplii and the numbers of cyprids in the present instance, as it is possible that the cyprids tend to occur in their greatest numbers close inshore.

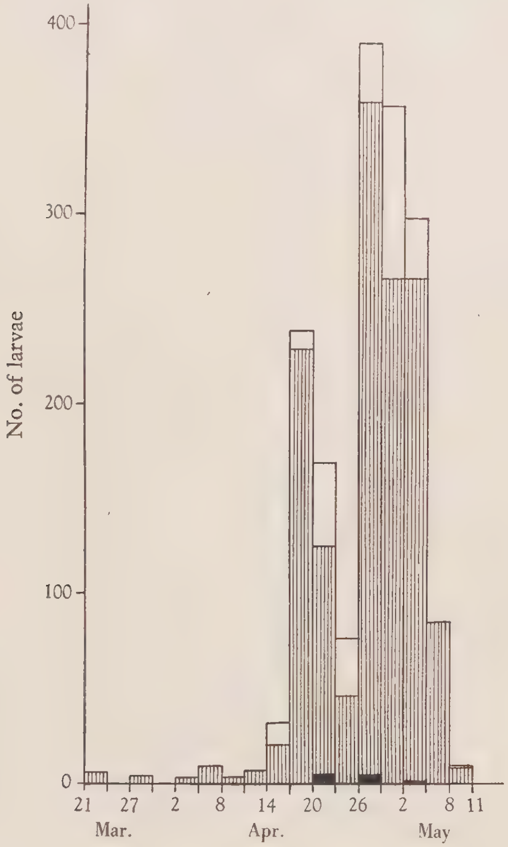

Fig. 15. Occurrence of cyprid larvae, Mar.–May 1946. Shading as in Fig. 14.

Some observations have been made on the dates when settlement of *B. balanoides* was first observed at different places. Fish (1925) states that in 1923 the first cyprids of this species appeared at Woods Hole on 8 February, that they were particularly abundant on 5 and 6 March and that they declined in numbers during April. He adds that the season in 1923 coincided exactly with that in 1900. This record is in general agreement with that of Grave (1933), who states that metamorphosis takes place between 15 February and 15 March. Moore (1935*a*) comments on the surprisingly small variation in the date on which the first settled cyprids were observed on the rocks at Port Erin. In 1932 this was 26 April, in 1933 and 1934 on 25 April. Runnström (1925) mentions that the first cyprids were observed in Liverpool Bay on 6 April and that these larvae reached their maximum on about 15 April.

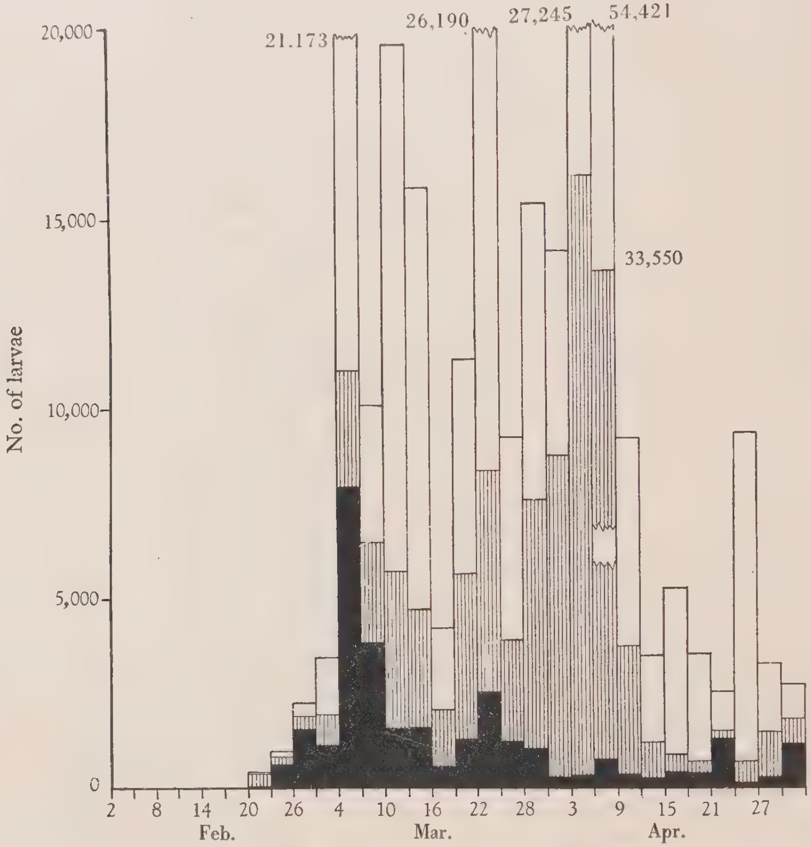

Fig. 16. Occurrence of Cirripede nauplii, Feb.–Apr. 1947. Shading as in Fig. 14.

Hatton & Fischer-Piette (1932), however, found considerable variation both in the date when settled cyprids were first recorded and in the length of the settlement period at St Malo. In 1930 the larvae first settled between 29 March and 2 April and settlement continued for 6 weeks, whereas in 1931 settlement first occurred between 15–21 February and 4–8 March, and this process continued for 3 months.

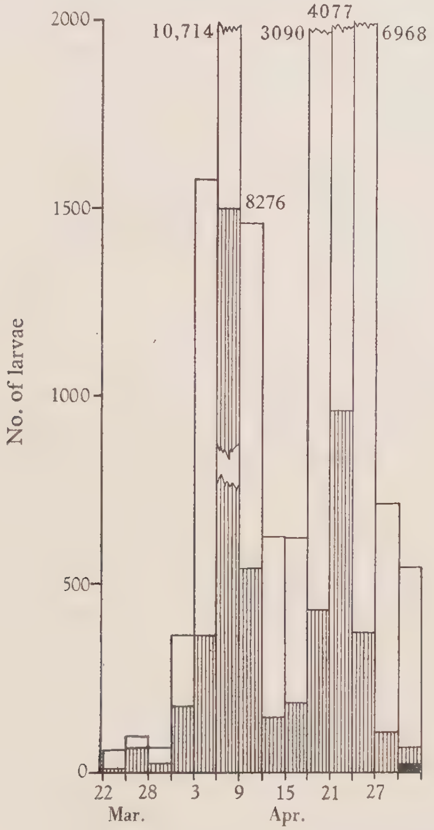

Fig. 17. Occurrence of cyprid larvae, Mar.–Apr. 1947. Shading as in Fig. 14.

The dates on which settlement was first observed and the period of settlement also varied to some extent in the present instance. Details are given below.

Year	Cyprids	Settlement
1944	First abundant on 3 April	Throughout April
1945	First abundant on 2 April	Limited to the first 2 weeks of April
1946	A few present from 14 April to the end of the month	Light settlement over last 2 weeks of April
1947	Some cyprids present throughout April; only abundant later in month	Light settlement throughout April; slightly heavier towards the end of the month

Thus it would appear that, in some places, settlement of *B. balanoides* occurs with some regularity on a given date (e.g. Port Erin, Woods Hole) whereas at others (St Malo, Millport) variations can occur from year to year. Characteristics have been observed in the course of the present survey which suggest a possible explanation of these differences.

Fig. 18 compares the general features of the planktonic occurrence of *B. balanoides* for 1944 and 1946; the former a year when heavy settlement occurred and the latter a year when settlement was light and when, in comparison with 1944, it occurred rather later. In 1944 heavy hauls of 1st and 2nd stage nauplii during the first half of March were succeeded by moderate hauls of later-stage nauplii later in that month and early in April. Cyprid larvae first appeared towards the end of March and were moderately abundant until towards the end of the following month. In 1946 the hauls over the earlier part of the *B. balanoides* season were of a similar order to those recorded 2 years earlier (though they were rather smaller) but the situation towards the end of March differed radically from that which occurred in 1944. Late-stage larvae were present only in very small numbers and no cyprid larvae appeared at all. This situation persisted until the middle of April when some later-stage nauplii appeared followed by cyprids in very small numbers. It would be dangerous to do more than speculate on the factors which virtually obliterated the later-stage nauplii and cyprids of *B. balanoides* in 1946, but the outstanding difference between the 2 years under discussion is the persistence, in 1946, of heavy diatom hauls well into April. The spring outburst of *Skeletonema* usually occurs at about the time when hatching of *Balanus balanoides* takes place; in 1944 heavy hauls of this diatom were confined to a short period in the middle of March and less interference with the larval sequence of *B. balanoides* was apparent (Fig. 18). In 1945, another year when cyprids of *B. balanoides* appeared in some numbers early in April, heavy hauls of *Skeletonema* were again confined to the middle of March. 1947, however, resembled 1946 more closely in that heavy diatom hauls persisted from early March until early April; it seems possible that settlement in 1947 was rather heavier than in the preceding year only because larval production was so much heavier. Reference has been made earlier in this paper to the lack of 'success' of the *Balanus balanoides* larvae which hatched early in March compared with those which hatched towards the end of the month; it may be surmised that the full development of the earlier 'brood' was appreciably upset by the abundance of diatoms in the water.

It would therefore seem possible that the marked regularity with which settlement occurs at Port Erin is correlated with the absence of heavy diatom hauls there since, according to Johnstone, Scott & Chadwick (1924), the heaviest diatom hauls do not occur there until May.

The absence of zooplankton in the presence of abundant phytoplankton is a phenomenon which has received a good deal of attention in recent years (Hardy & Gunther, 1935; Harvey *et al.* 1935; Lucas, 1936). It is therefore of interest to note this example provided by the larval stages of *B. balanoides*, of

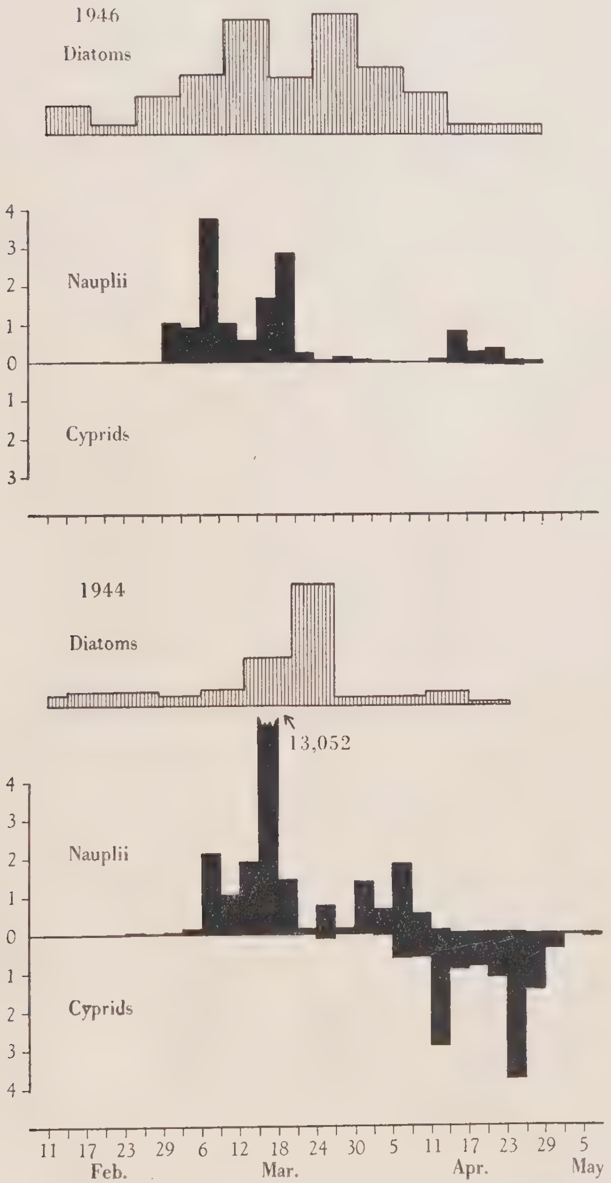

Fig. 18. Occurrence of larval stages of *Balanus balanoides*, 1944 (below) and 1946 (above), compared with estimates of diatom density in the two years. Histograms of the numbers of nauplii present over 3-day periods are shown extending upwards, those of the numbers of cyprids present extending downwards, from the base line. Numbers of nauplii and cyprids expressed in thousands; diatom abundance on an arbitrary scale.

the apparent effect of heavy phytoplankton on a zooplankton species, particularly as the absence of settled cyprids is useful confirmatory evidence of the absence of settling stages as indicated by plankton hauls. Further, it is also of interest to note that this interference seems far less effective for the larvae of *B. crenatus*. In an earlier section of this paper attention has been drawn to the closer correspondence between the numbers of early nauplii and the numbers of cyprid larvae for this species in 1947 and this relation may be compared with that obtaining for *B. balanoides*. In 1946 the situation was perhaps even more striking. The period from mid-March to mid-April, when diatom hauls were generally heavy, was characterized not only by the virtual absence of *B. balanoides* but also by the existence of a similar state of affairs for *B. crenatus*. Yet, although the later-stage nauplii and the cyprid larvae of this species were not recorded in plankton hauls, there is clear evidence, from surfaces immersed over this period, that a settlement of *B. crenatus* occurred at the beginning of April. Thus plankton hauls alone would have indicated the absence of both species: with *B. balanoides* this indication was probably correct (to judge by the absence of settlement, a condition which, it should be noted, obtained over a considerable area of the Clyde shores and was not purely a local phenomenon), but with *B. crenatus* settling stages were, in fact, present. It should be possible to test this suggested difference between the larvae of *B. balanoides* and those of *B. crenatus* experimentally; it is hoped that it will be possible to carry out work along these lines at some time in the future.

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The author is indebted to the Marine Corrosion Sub-Committee of the British Iron and Steel Research Association for permission to publish these notes and to Prof. J. E. Harris for his interest in and encouragement of this work. He also wishes to acknowledge the help received from other members of the team working on the fouling problem, particularly Miss J. C. Mott and Mr M. W. H. Bishop. To the Director of the Marine Station, Mr R. Elmhirst, the author is indebted, not only for his helpful criticism of this paper in manuscript but also for his many useful suggestions during the course of this work. Acknowledgement is also made to his assistant, Miss E. H. Osborne, for her help in the labour of counting and recording and in preparing the diagrams for this paper.

SUMMARY

In the course of some 4 years' work on the biology of fouling organisms, observations have been made on aspects of the general biology of *Balanus balanoides*, *B. crenatus* and *Verruca stroemia*.

Observations on the state of development of the ova within the mantle cavity of *B. balanoides* and of the occurrence of the larvae in the plankton indicate that hatching takes place during the first fortnight in March, that the later-stage nauplii are abundant during the second half of that month and that the cyprid larvae may become abundant during April. The larval sequence is not always completed successfully; conditions which seem inimical are discussed.

Factors which seem to be of importance in affecting settlement of *B. balanoides* are discussed. The presence of other organisms is an adverse factor, though the potency of this factor is probably not the same for all organisms; the presence of slime can prevent settlement and, though evidence can be quoted in support of heavier settlement on shaded surfaces, it is emphasized that the operation of other factors may have brought about this result. The proportion of the tidal cycle during which current speeds are not too high to prevent settlement seems likely to be important.

Provided that other conditions are favourable *B. balanoides* settles readily on surfaces continuously immersed and individuals which settle under these conditions grow more rapidly, at least for the first few months after settlement, than their contemporaries on the shore.

The larvae of *B. crenatus* appear in the plankton rather earlier than those of *B. balanoides*, but the time taken to complete the larval sequence from the 1st stage nauplius to the cyprid is roughly the same as that for the latter species, namely 1 month. In *B. crenatus*, however, hatching is not limited to a short period during March but continues at intervals through the summer. There are indications that the successful completion of the larval sequence of this species is less affected by an abundance of phytoplankton than is that of *B. balanoides*.

Settlement of *B. crenatus* is periodic and individuals which settle early in the spring can attain practically their full size (28–30 mm. basal length) during the same season. Growth during the summer takes place at average rates which vary from 0·1 to 0·2 mm. increase in basal length per day. Growth is negligible during the winter months.

Specimens of *B. crenatus* which settle early in April contain developing ova by the beginning of July, so that spring-settled forms can produce larvae which themselves may settle before the end of the summer.

Observations on *Verruca stroemia* have been limited to the occurrence of the larvae in the plankton. Like those of *Balanus crenatus*, the larvae of *Verruca stroemia* are present at intervals through the summer. Early-stage nauplii of this species may dominate the plankton early in the year, but no correspondingly heavy hauls of later-stage nauplii have been recorded. Possible explanations of this discrepancy are discussed. The cyprid never occurs in any numbers in surface hauls.

Incidental observations on the planktonic occurrence of the nauplii of *Sacculina* (probably *S. carcini*) and of *Peltogaster paguri* are given.

Details are given of the abundance of all Cirripede larvae in the plankton for the years 1944–47 which emphasize the extent of variation that can occur from year to year.

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THE EFFECT OF NARCOTICS ON THE ENDOGENOUS RESPIRATION AND SUCCINATE OXIDATION IN OYSTER MUSCLE

By George Frederick Humphrey

Department of Biochemistry, University of Sydney, Australia

(Text-figs. 1–6)

Introduction

The adductor muscles of Lamellibranchs present unusual features in their physiology. Thus it has been known for some time (Marceau, 1909) that they are able to support relatively large tensions, and the morphological differentiation into nacreous and vitreous parts in some species has led various workers (Parnas, 1910; Boyland, 1928; and Kobayashi, 1929) to attempt to correlate differences in metabolism with these properties. Also, Riesser (1933) has investigated, by the usual pharmacological techniques, the action of a number of compounds on invertebrate muscle, and concluded that these smooth muscles behaved similarly to cross-striated frog muscle. More recently, some features of the glycolytic mechanism (Humphrey, 1943) and of the succinoxidase system (Humphrey, 1947) in the adductor muscles of *Saxostrea commercialis* have been established. It was shown that succinic acid was able to increase the oxygen consumption considerably, and the effects of various inhibitors on the oxygen uptake in the presence and absence of succinic acid were determined.

In continuation of this, it was thought desirable to determine the effects of other classes of inhibitors on the oxygen consumption, and, with this object in view, the action of narcotics was studied. The effect of narcotics on the oxidation of succinic acid was also determined, since succinic acid plays such a central role in tissue metabolism (Szent-Györgyi, 1937). Also, Quastel & Wheatley (1933) have found that, in general, the oxidation of succinic acid by brain tissue is, unlike the oxidation of numerous other substrates, insensitive to the presence of narcotics; it therefore becomes important to determine if such insensitivity occurs with the muscle taken from *Saxostrea*.

Materials and Methods

Specimens of *Saxostrea commercialis* were obtained from the C.S.I.R. Experimental Farm at George's River, Sydney, Australia; only adult animals, 2–3 years old, were used.

The narcotics were used as neutralized aqueous solutions. Salicylamide was prepared by the method of Anschütz (1919); the other compounds were chemically pure commercial specimens.

Cytochrome was prepared from pig heart by the method of Keilin & Hartree (1937), but was dialysed against distilled water (Potter, 1941).

The adductor muscles, immediately after dissection, were homogenized at a 30% concentration with water in the instrument previously described (Humphrey, 1946). The desired amount of narcotic in 2 ml. of water was placed in a manometer flask, together with neutralized sodium succinate (to give a final concentration of 0·05 M) if the oxidation of this substance was being studied. 2 ml. of the muscle suspension was then pipetted into the flask, and the oxygen consumption measured under the conditions already given (Humphrey, 1946). When used, cytochrome was added directly to the main compartment of the manometer flask, to give a final concentration of 10^{-5} M.

RESULTS

The main results are set out in Figs. 1–6, and Table I. Two or three concentrations of each narcotic were studied, depending on the solubility of the compound in question. Included with each set was a control with water in place of narcotic, and oxygen consumption was always recorded at 1 and 2 hr. Using the 2 hr. reading, the inhibition was then calculated as a percentage of the control, and the mean of several values graphed against the concentration of narcotic or the logarithm of the concentration.

TABLE I. EFFECT OF URETHANES, SALICYLAMIDE, AND CHLORAL HYDRATE

Inhibition (%) by	...	Endogenous	Endogenous + cytochrome	Succinic acid	Succinic acid + cytochrome
Urethane	0·001 M	6	5	15	9
	0·01 M	18	15	21	14
	0·05 M	−6	−6	30	17
Phenyl urethane	0·001 M	30	39	33	20
	0·005 M	47	56	54	60
Salicylamide	0·001 M	10	15	29	33
	0·01 M	50	54	63	70
Chloral hydrate	0·001 M	25	15	13	10
	0·01 M	50	38	64	41

On the whole, straight lines are obtained when the logarithmic plotting is used, but sometimes (Figs. 5 and 6) the inhibition is directly proportional to the concentration. These differences may be compared with the sigmoid curves obtained by Jowett & Quastel (1937). Replacement of the carboxyl group of benzoic acid with an acid amide group always increases the inhibition, but the reverse is true for salicylic acid and salicylamide. At equal concentrations, phenyl urethane is a better inhibitor than ethyl urethane, and the latter, at a concentration of 0·05 M, causes a slight increase in the oxygen consumption.

All the narcotics inhibit succinate oxidation, and usually more strongly than the endogenous respiration. On the whole, the addition of cytochrome does not affect the inhibition of the endogenous or succinate respiration; marked exceptions are the effects on the endogenous respiration of 0·025 M barbitone, where the inhibition drops from 48 to 20% (Fig. 5), and 0·05 M morphine,

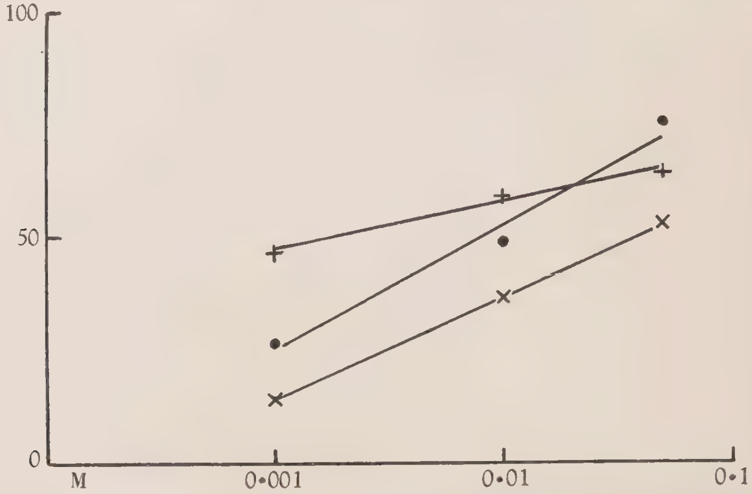

Fig. 1. Effect on endogenous oxygen consumption. Ordinates are percentage inhibition; abscissae, molarity of narcotic. • benzamide; + salicylate; × benzoic acid.

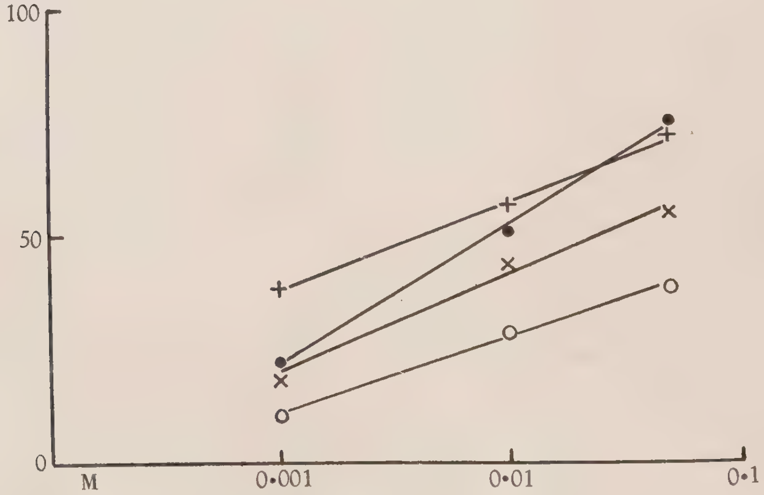

Fig. 2. Effect on endogenous oxygen consumption in the presence of cytochrome. Ordinates are percentage inhibition; abscissae, molarity of narcotic. • benzamide; + salicylate; × benzoate; ○ morphine.

where 67% changes to 40% after the addition of cytochrome (Fig. 6). The variations in inhibition caused by the addition of cytochrome and/or succinate

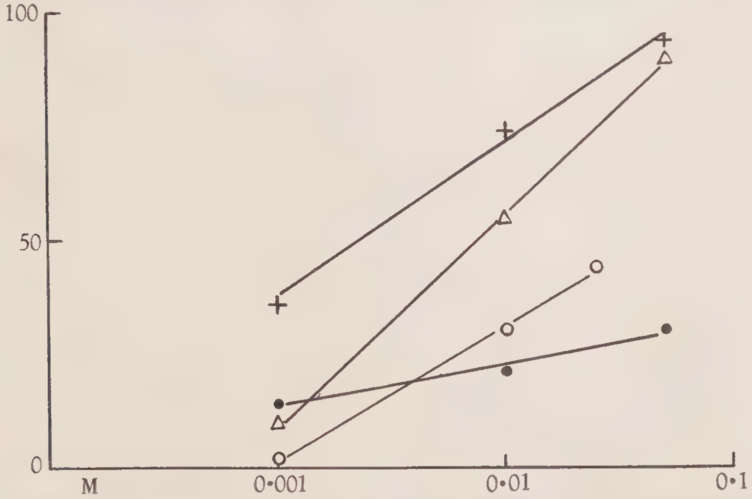

Fig. 3. Effect on succinate oxidation. Ordinates are percentage inhibition; abscissae' molarity of narcotic. + salicylate; △ caffeine; ○ barbitone; • urethane.

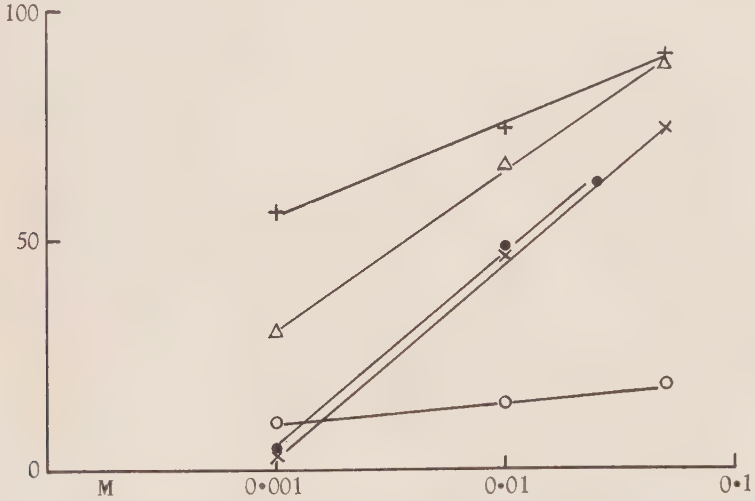

Fig. 4. Effect on succinate oxidation in the presence of cytochrome. Ordinates are percentage inhibition; abscissae, molarity of narcotic. + salicylate; △ caffeine; × benzoate; • barbitone; ○ urethane.

may be due to the fact that in the endogenous respiration several systems are functioning at more or less similar rates, whereas, after these additions, certain pathways become more prominent.

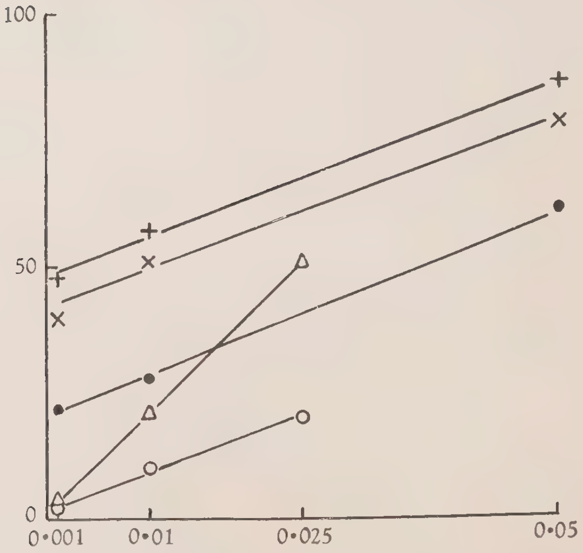

Fig. 5. Effect on endogenous oxygen consumption. Ordinates are percentage inhibition; abscissae, molarity of narcotic. + caffeine in the presence of cytochrome; × caffeine; △ barbitone; • morphine; ○ barbitone in the presence of cytochrome.

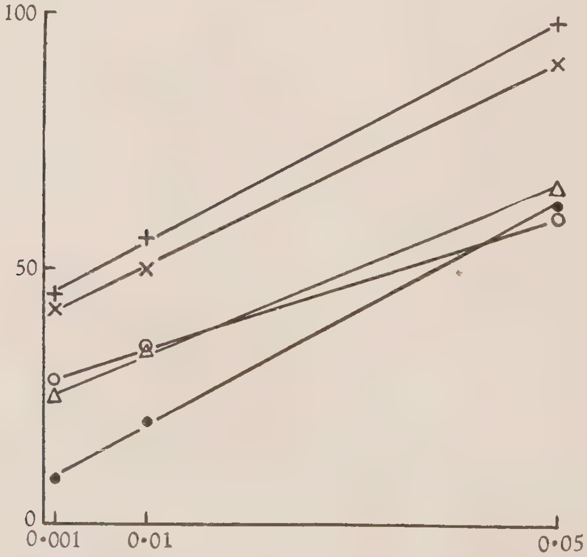

Fig. 6. Effect on succinate oxidation. Ordinates are percentage inhibition; abscissae, molarity of narcotic. + benzamide in the presence of cytochrome; × benzamide; △ benzoate; • morphine; ○ morphine in the presence of cytochrome.

It was not possible to increase the inhibition by incubation of the tissue suspension and narcotic for 30 min. before tipping in the succinate from a side arm. Similar incubation of the tissue and succinate, followed by the addition of narcotic, gave slightly less inhibition. This could be interpreted by assuming that there was substrate-narcotic competition for a definite site of attachment in the suspension.

Discussion

Keys (1937) has stated that it is a 'fundamental fact that narcotized cells no longer show or transmit irritable impulses...in narcotic doses, true narcotics do not seriously interfere with the total resting metabolism of the cell'. Since it is not known what a 'narcotic dose' for *Saxostrea* is, it is not possible to deny or affirm the latter part of this statement. Also, in general, it is desirable to reserve the concept of narcosis for the action of certain classes of substances on whole organisms, or cell preparations which approximate closely to physiological conditions. The system studied here can be regarded as 'intermediate' (Clark, 1937) and the use of the term narcotic must be regarded as a convenient way of designating a type of compounds.

The most widely accepted explanation of the action of narcotics on cells is the Meyer-Overton theory which seeks to correlate the activity with the solubility of the narcotic in lipoid phases. However, this does not give an explanation of the phenomena observed with partially isolated enzyme systems. Michaelis & Quastel (1941) investigated the effect of chloretone on various dehydrogenase systems, and came to the conclusion that this narcotic has its effect mainly on flavoprotein, or an unknown component intermediate between flavoprotein and cytochrome oxidase. Östergren (1944) suggests that narcotics can associate with the lipophilic side chain of polypeptides and change the folding pattern; perhaps this is how chloretone affects the flavoprotein. However, there is no conclusive evidence for these theories, and the action of a given narcotic seems to vary from one organism to another, suggesting that there is more involved than a relatively simple relationship between narcotic and chemical grouping.

Endogenous Oxygen Consumption

Urethanes have been used extensively on different organs and isolated respiratory systems. Warburg (1914) showed that phenyl urethane was a more powerful inhibitor of erythrocyte respiration than ethyl urethane. Krogh (1915) demonstrated that ethyl urethane is suitable for narcotizing various marine animals; in general 0·05–0·1 M was sufficient. Navez, Crawford, Benedict & Dubois (1941), working on the oxygen consumption of the heart of *Venus mercenaria*, showed that 0·01 M urethane caused an increase of 20%. Moog & Spiegelman (1942) found that neither ethyl nor phenyl urethane affected the oxygen uptake of stems cut from *Tubularia*. However, Barnes

(1944) obtained an inhibition of the respiration of developing eggs of *Rana pipiens* with 0·2 M urethane. Nothing similar to the break in activity-concentration relationship found with *Saxostrea* muscle has been previously observed in animal tissue.

Cheney (1946) obtained 60% inhibition of the oxygen uptake of fertilized *Arbacia* eggs in the presence of 0·1 M caffeine. He concluded, with little direct evidence, that caffeine acts on the cytochrome oxidase. On the whole, caffeine is one of the most effective narcotics for inhibiting the endogenous respiration of *Saxostrea* muscle.

Regarding the effects of the narcotics studied here, there has not yet been reported any other information with which it would be possible directly to compare the findings obtained with *Saxostrea*. However, Shideman & Seevers (1941), using rabbit muscle, found that 0·00017–0·0017 M morphine increased the oxygen consumption. No such acceleration was observed with *Saxostrea* muscle when 0·001–0·05 M morphine was used.

Oxidation of Succinic Acid

Assuming that added succinic acid causes an increase of about 300% in the oxygen consumption (Humphrey, 1947), an examination of Figs. 1–6 reveals that the oxidation of succinic acid is inhibited by all the narcotics used. Only with 0·001 M benzoic acid and 0·001 M chloral hydrate is the oxidation uninhibited, and this only in the presence of added cytochrome. These findings are in direct contrast to those of Quastel & Wheatley (1933), Jowett & Quastel (1937) and Seevers & Shideman (1941), who found that, for vertebrate tissue, the oxidation of succinic acid is unaffected by a large number of narcotics when these are present in concentrations of about 0·01 M.

Also, Greig (1946), basing her arguments on the work of Jowett & Quastel (1937) and Michaelis & Quastel (1941), i.e. on the insensitivity of the oxidation of succinate to narcotics, showed that the site of action of nembutal is the flavoprotein-cytochrome *b*-link of the respiratory chain; these experiments were with yeast and brain and cannot be directly compared with observations on invertebrate tissue.

CONCLUSIONS

As might be expected, the effects of narcotics on *Saxostrea* muscle differ quantitatively from those obtained with vertebrate muscle. In addition, there are two qualitative differences; namely, the break in activity-concentration relationship shown with urethane, and also the inhibition of the oxidation of succinic acid. In these two respects, *Saxostrea* muscle is distinguished from other tissues.

However, it is not possible to conclude that the role of succinic acid in the metabolism of the adductor muscle differs fundamentally from that in other muscle. Also, the changes in narcotic effect due to the presence of added cytochrome are not sufficiently definite to indicate that the metabolic pattern is changed by added cytochrome. With regard to the site of action of the narcotics used, definite conclusions must await an elucidation of the main respiratory pathways operating in this invertebrate tissue.

SUMMARY

The action of the following compounds on homogenates of the adductor muscles of *Saxostrea commercialis* was studied: urethane, phenyl urethane, chloral hydrate, salicylic acid, morphine, caffeine, barbitone, benzoic acid, salicylamide and benzamide.

It was found that, except for 0·05 M urethane, the endogenous oxygen consumption was reduced by all these compounds when present in concentrations ranging from 0·001 to 0·05 M. The oxidation of succinic acid was partially inhibited by these substances.

These findings are discussed in relation to similar studies on other tissues.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

THE PEDAL SUCKER and ANAL GLAND OF SOME BRITISH STENOGLOSSA

By Vera Fretter

Proc. Malacol. Soc., Vol. 27, 1946, pp. 126–30

In *Ocenebra erinacea* (L.), *Nucella lapillus* (L.) and *Urosalpinx cinerea* (Say) the foot possesses a small disk-shaped, retractile sucker, situated mid ventrally, immediately behind the anterior pedal gland. Its movement is controlled by muscles and blood pressure, which keep it turgid when protruded. It is covered by ciliated glandular epithelium. The amount of secretion is scanty and has no solvent effect on mollusc shells. The sucker grips the shell of the prey below the spot where the proboscis is working and seems to steady its base.

The rectal gland of these carnivorous stenoglossa develops as a simple diverticulum from the gut, and appears to act as an accessory kidney. The epithelium abstracts excretory matter from the blood and builds it up into masses which can be easily passed from the body. V.F.

MARINE SEISMIC PROSPECTING

By M. N. Hill and P. L. Willmore

Nature, Vol. 159, 1947, p. 707

Considerable progress was made before the war in the use of seismic refraction shooting for the study of submarine geology. Two ships were used in this work, one of which fired the charges at varying distances from the second, on which was the recording gear connected to geophones on the sea bed. The difficulty of placing these instruments on the sea bed in depths greater than 100 fathoms limited the work to the continental shelf. As a result of this limitation, experiments were undertaken during the winter of 1947 to ascertain whether hydrophones at a depth of about 100 ft. compared favourably in their response with geophones laid on the bottom. The difficulties involved in obtaining two ships for this work were overcome by using a buoy for firing the charges, or, for the shorter shots, by trailing the charges on a long buoyant electric cable.

The conclusions from this work were first, that a hydrophone gave a response at least as good as that of a geophone, and secondly, that the charge-firing buoy was unsatisfactory since the instant of detonation was uncontrollable after the buoy had been launched, and because of the necessarily complicated safety precautions. For long range work it would therefore be necessary either to use two ships, or to attach the hydrophone to a radio buoy which would transmit the sounds to the firing ship. M.N.H.

Contribution to the Study of the Sponges

By Margaret W. Jepps

Proc. Roy. Soc., London, B, Vol. 134, 1947, pp. 408–17

The old observations of H. J. Carter and others on the contractile vacuoles of sponge cells have been questioned in recent years. The presence of contractile vacuoles is here established in both amoebocytes and choanocytes of the fresh-water sponges; but they have not been seen in the cells of several marine sponges, though figured by some of the older authors. Methods are described for observing the vacuoles, and incidentally other activities of the cells also.

Young sponges grown from gemmules were very useful in these studies and it was found possible to have them throughout the winter months by a simple process of vernalization.

Attention is drawn to the importance of these observations in any consideration of the relationships of the Porifera to the Protozoa and to the Metazoa respectively. M.W.J.

Giant Nerve Fibre of *Myxicola infundibulum* (Grube)

By J. A. C. Nicol and J. Z. Young

Nature, Vol. 158, 1946, p. 167

It has been known for some time that the Sabellid *Myxicola* possess very large nerve fibres, and investigations confirm that these may reach 1 mm. in diameter in the contracted state of the worm. The fibre extends throughout the length of the ventral cord and is a single unit maintained by many cell bodies scattered along its length. The fibre originates in the supra-oesophageal ganglia from two especially large cells. Branches given off along its length proceed to the muscles. There is a connective tissue sheath not containing any visible myelin.

Evidently the fibre constitutes a final common path by which afferent impulses from any part of the body activate all the longitudinal muscle fibres, producing the quick movements and withdrawal characteristic of the animal. J.Z.Y.

THE MECHANICS AND INNERVATION OF THE STARFISH TUBE FOOT-AMPULLA SYSTEM

By J. E. Smith

Phil. Trans. Roy. Soc., London, B, Vol. 232, 1946, pp. 279–310

A tube foot with its attached ampulla is a reciprocally acting self-contained system. The ampulla has a fluid capacity just adequate to produce, on contraction, the observed maximal degree of protraction of the foot. There is no evidence that water enters or leaves the system by way of the radial water canals during extension or withdrawal of the foot. Further aspects of the mechanics of movement of the foot and ampulla are considered in relation to the arrangement and properties of their constituent muscles and connective tissue.

An account, based on the results of *intra-vitam* methylene blue staining, is given of the nervous arcs that supply the muscles of the system. The sensory and associative fibres of the foot are described and their connexions with the association tracts of the radial nerve cord followed. The foot and ampulla muscles are innervated by axons whose cell bodies lie in one or other of two centres situated in the foot, near the entrance to the ampulla neck. One centre, laterally situated, appears to be excited directly through the association pathways of the foot; the more medial centre, on the other hand, has central connexions with the radial nerve cord through a system of neurones whose cell bodies lie above the cord in the floor of the radial perihaemal canal.

Some implications of the double innervation (central and peripheral) of the foot-ampulla are discussed. J.E.S.

CONTRIBUTIONS TO THE BIOLOGY OF THE MACKEREL, *SCOMBER SCOMBRUS* L.: MACKEREL MIGRATIONS IN THE ENGLISH CHANNEL AND CELTIC SEA

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By G. A. Steven, B.Sc., F.R.S.E.

Zoologist at the Plymouth Laboratory

(Text-figs. 1–6)

INTRODUCTION

The common mackerel (*Scomber scombrus* L.) is one of the important European food fishes. Forty-two species of commercial sea fishes are listed by the Conseil Permanent International pour l'Exploration de la Mer in its *Bulletin Statistique des Pêches Maritimes* as being landed in northern and western Europe. Four-fifths of these landings are made up of only twelve important food fishes, of which the mackerel is one. In 1937 (Thompson, 1939), the last year for which full normal figures are available,[1] approximately 1¼ million cwt. of mackerel were landed by all the countries of northern and western Europe (excluding Russia), having a total value, as nearly as can be ascertained, of just over £887,000. To this total Great Britain, Eire, and Northern Ireland contributed rather more than 14% of the quantity and almost 13% of the value. During the inter-war period, however, Britain's contribution had fallen steadily, her share in 1913 (a year that has long been used as a standard of comparison) being no less than 49% of the total quantity and 31% of the total value of all mackerel landings.

Of the British Islands, England is the chief mackerel-fishing country. Just prior to the outbreak of the recent war her total landings were some 140,000 cwt. valued at about £80,000. It is a noteworthy fact that rather more than one-third of this quantity was landed at the single small port of Newlyn, in Cornwall (Figs. 1 and 2). It is still more surprising to note (Fig. 1) that during the four years 1923–1926 more mackerel were landed at Newlyn than at all other ports in England and Wales put together.

There are, in normal times, two distinct mackerel fisheries worked from Newlyn. One is a long-distance, deep-sea fishery carried out by steam drifters (of the normal herring drifter type) in the Celtic Sea far to the westward of the Scilly Islands—except towards the end of the season when fishing takes place nearer land. This fishery will be called the *Newlyn Deep-Sea Fishery* for

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[1] The figures for 1938, though published in 1944, are not complete.

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mackerel. The other is an inshore fishery that takes place in inshore waters off the northern coasts of the Cornwall and Devon peninsula. In it, boats from other small ports take some part, but Newlyn is the chief centre. This fishery will therefore be called the *Newlyn Inshore Fishery* for mackerel.

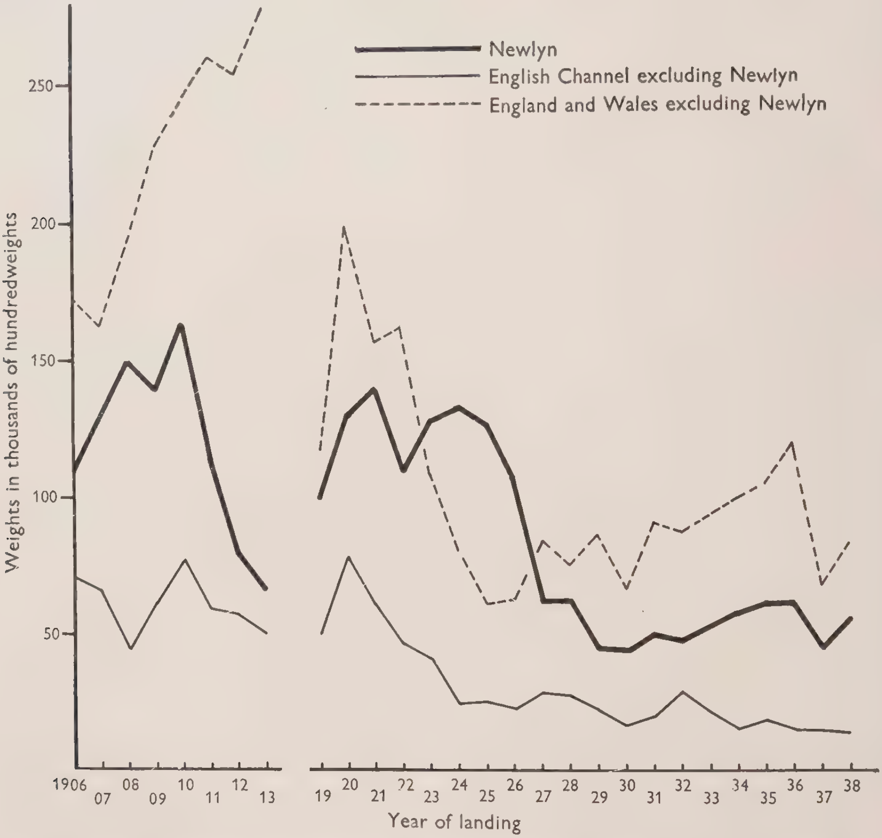

Fig. 1. Mackerel landings in thousands of hundredweights at Newlyn (——); in England and Wales excluding Newlyn (----); and at English Channel ports excluding Newlyn (——). From *Sea Fisheries Statistical Tables* for the years 1906–1938 inclusive.

At Newlyn, then, in normal times, by far the most important mackerel fishery in Great Britain takes place, and it was at this port that most of the data for this investigation were collected.

The Newlyn mackerel fisheries were temporarily suspended during the 1914–18 war and again in the Second World War. Unfortunately, normal fishing has not yet been resumed after this second interruption owing to the uneconomic prices obtainable for mackerel in comparison with operating costs.

In past years there was also a flourishing mackerel fishery farther up the English Channel at Plymouth; but the Plymouth fishery, for purely economic reasons, gradually declined and came entirely to an end about the year 1926. This fishery will be called the *Plymouth Channel Fishery* for mackerel. A brief but detailed description of all these fisheries will now be given because an adequate knowledge of them is necessary for obtaining a clear picture of the migratory movements of the mackerel upon which they all depend.

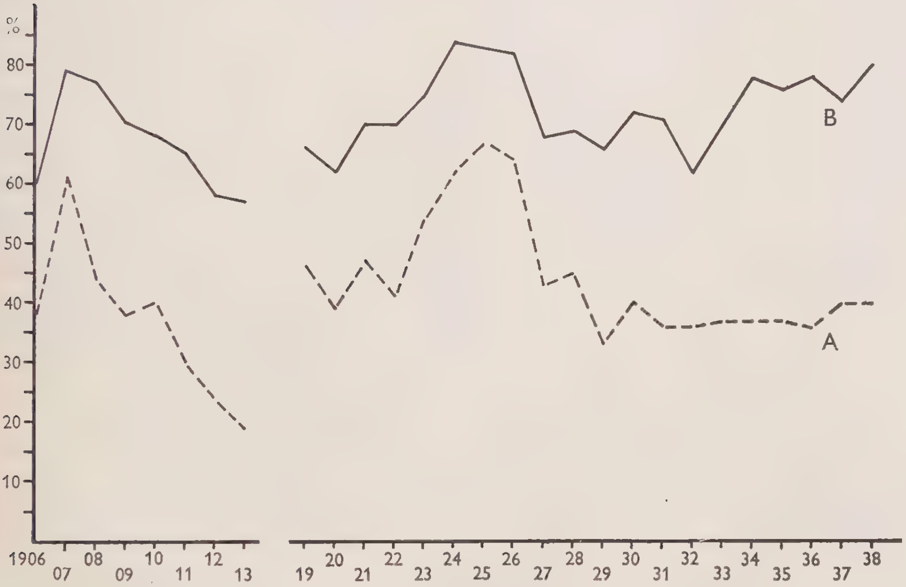

Fig. 2. Percentage contribution by Newlyn to total landings (*A*) in England and Wales; (*B*) at English Channel ports, from 1906 to 1938 inclusive.

The Plymouth Channel Fishery

Although this fishery no longer exists, it is necessary to examine its previous activities in considerable detail, for mackerel are still present on the grounds worked by it long ago and the same migrations still take place by fish that are now untouched by any catching instrument.

The mackerel season began off Plymouth towards the end of December or early in January and boats from east and west used to converge on the port in large numbers to take part in it. Ridge (1889, p. 72), reporting on the fishery of 1888, states that fishing began in that year in January and that vessels from Yarmouth, Lowestoft, Newhaven, Brighton, Eastbourne, Hastings, Porthleven, Newlyn, and Mousehole arrived to take part in it. According to Calderwood, (1892, p. 279) the Plymouth drift-net fleet alone at this season used to number between three and four hundred sail.

In a series of reports on fishing in the neighbourhood of Plymouth, in different months of each year towards the close of last century (1892 and 1893),

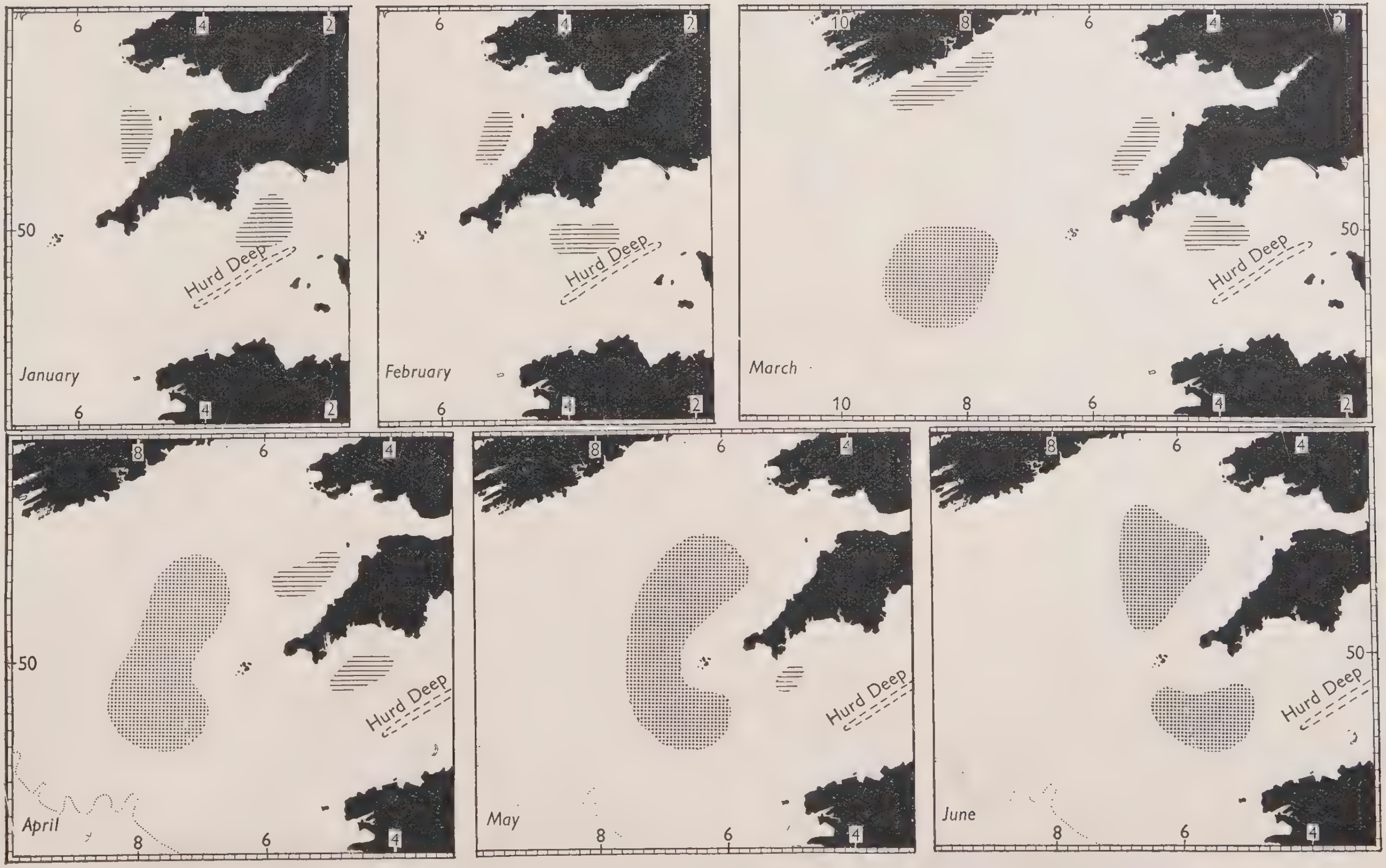
January
February
March
April
May
June
Hurd Deep
50
10
8
6
4
2

Fig. 3. Generalized charts showing times of fishing for mackerel in different parts of the English Channel and Celtic Sea. *Hatched* areas, inshore fisheries; *stippled* areas, deep-sea fishery (*vide* pp. 519–24). The 100-fathom contour is indicated by a dotted line.

Calderwood constructed a series of monthly charts showing as nearly as possible the kinds of fish caught during each month and the positions of the grounds being worked. From these reports, and from conversations with some of the old fishermen who were active at that time, one finds that in January fishing for mackerel took place on grounds to the eastward of Plymouth, generally from 10 to 30 miles south to south-west of Start Point. As the season advanced the fish had to be sought progressively farther and farther to the westward. By the middle or end of March the fleet would be working from 10 to 30 miles southward from the Eddystone lighthouse (i.e. 20–40 miles to the seaward of Plymouth). By May the best catches were generally to be had on grounds still farther west, and the Plymouth fleet sometimes went as far as 40 miles south-west of Lizard Head before terminating the season's fishery. The time at which this occurred varied from year to year, but was seldom if ever later than the middle or end of May. When this happened many of the east coast boats returned to their home ports to fish no more for mackerel until another 'west-country season' came round. But some of them, together with the west-country boats, proceeded to Newlyn and other Cornish ports to carry on fishing from there on the deep-sea grounds to the westward of the Scilly Islands (*vide* p. 522). This sequence of events in the Plymouth fishery is summarized in Fig. 3 in which the hatched area in the English Channel indicates the extent of the fishing ground and the gradual shift of the fishery from its eastern end in January to its western extremity in May.

It should be noted that these west-going shoaling fish never approach really close to the land, but always remain at some distance from it. This is in marked contrast to what happens when mackerel reappear in the Channel in June after the shoals have broken up (*vide* p. 524). The fish then appear hard by the beaches and in creeks and harbours all along the shoreline in the very shallowest water.

The Newlyn Inshore Fishery

This fishery is confined to inshore grounds along the north Cornwall and north Devon coast. On these grounds, extending roughly from 20 to 50 miles north-north-east of the Longships Lighthouse (Land's End), fishing in normal times begins in December or early January and continues for 3 or 4 months. At the beginning of its season the best catches are to be expected well to the northward and then progressively farther southward as the season advances. The hatched area to the north of the Cornwall-Devon peninsula in Fig. 3 indicates the extent of this fishing ground and the gradual shift of the fishery from its northern end in January to its south-western extremity by about April.

The sequence of events in this area should be carefully compared with that on the fishing grounds in the English Channel (also shown on this chart and already described) and their similarity noted.

The Newlyn Deep-Sea Fishery

The modern great spring mackerel fishery from Newlyn opens in March (Fig. 3) on grounds right out in the open Atlantic far to the westward of the Scilly Islands. It is a drift fishery carried on by steam drifters of the familiar herring-drifter type which come to this port from the east coast ports of Yarmouth and Lowestoft.

Although fishing begins in the first days of the month, it is usually somewhere about the middle of March before the fleet falls in with the main shoals. While the search for them is going on, some of the boats try their luck hard by the Irish coast to the south-west and south of Ireland. From 10 to 20 miles south to south-west of Fastnet Rock and about the same distance off Galley Head and the Old Head of Kinsale are the most favoured localities; and good catches are sometimes made there, but for only a very short time at the beginning of the season (Figs. 3 and 4 A).

The charts in Fig. 4 have been prepared to show the locus of this fishery as indicated by the activities of ten drifters out of a total fleet of twenty-four in 1938—a typical year. The information upon which the charts are based was derived from log-book records kept by each vessel. Every shot made by each of the ten drifters throughout the season is indicated by a dot in the position in which it was made. The fishing of these ten vessels is fully representative of that of the total fleet and gives a true picture of the changes in the locus of the fishery as the season advanced.

It will be seen (Fig. 4 A) that during the first fortnight of March—the opening fortnight—there was only limited fishing, concentrated chiefly near the south coast of Eire. A few exploratory tries were also made over a widely scattered area to the westward of the Scilly Islands. This 'scatter' indicates the absence of good fishing in that locality as yet. By the second half of March (Fig. 4 B) fishing is in full swing with the area of chief fishing intensity located from 70 to 100 miles west to west-south-west of the Bishop Rock, Isles of Scilly. During the first half of April (Fig. 4 C) the best fishing still persists in approximately the same place but slightly less distant. A few tries were also made on northern grounds about 70 miles north-north-west of the Longships (Land's End), but failed to find many fish. By the second half of April (Fig. 4 D) the locus of chief fishing intensity had moved to these northern grounds, all the vessels having for the time being forsaken the 'southern' grounds. During the first half of May (Fig. 4 E) good catches were being taken to the westward of Scilly, but considerably closer to land (i.e. farther to the eastward) and on a slightly more southerly bearing. After the middle of the month (Fig. 4 F) most fish were encountered still farther in towards the mouth of the English Channel, and, being productive of good catches, attracted most of the fleet to this locality. During the first half of June (Fig. 4 G) fish were being caught both to the northward of Scilly and southward from Mounts Bay, the northern

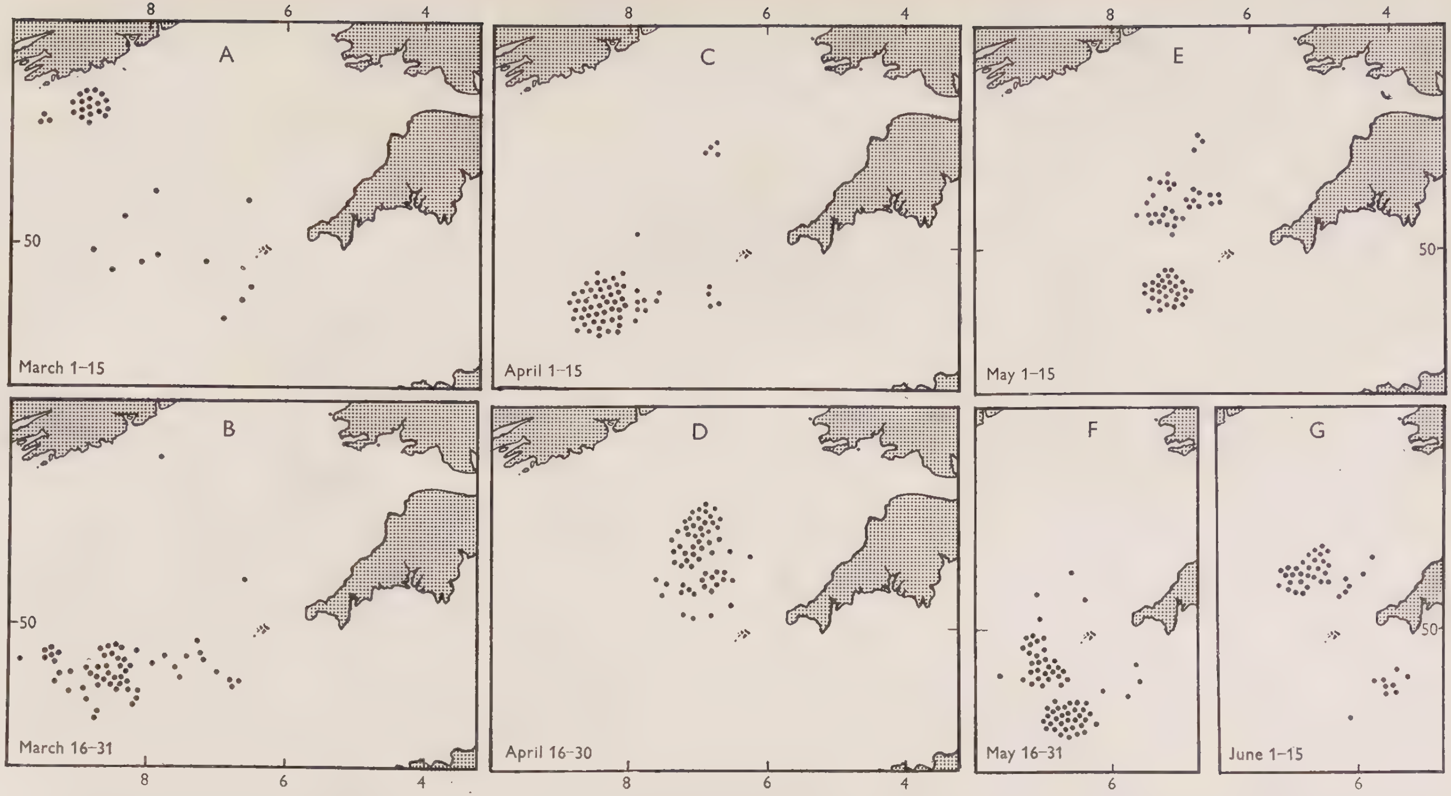
A
B
C
D
E
F
G
March 1–15
March 16–31
April 1–15
April 16–30
May 1–15
May 16–31
June 1–15
8
6
4
50

Fig. 4. Locus of mackerel fishing in 1938 by Newlyn-based steam drifters; A, in the first half of March; B, in the second half of March; C, in the first half of April; D, in the second half of April; E, in the first half of May; F, in the second half of May; G, in the first half of June. Each dot represents a 'shot' by one of ten selected drifters.

locality yielding the better catches on the average and therefore attracting the greater part of the fleet. But all catches were now dwindling; on 15 June the last drifter landed its final catch and all the fishing stopped.

Although the changes in the locus of the fishery depicted in Fig. 4 A–G are typical of what happens each year, no two seasons are ever quite the same. In some years, towards the end of the season, best fishing is obtained to the northward of the Scilly Islands; in other years the western end of the English Channel provides the best catches. By about the middle or end of June in every season drift fishing comes to an end, the shoals having so dispersed that this method becomes unremunerative. It is at this time that the mackerel appear in large numbers in shallow waters all along the shores of southern and western England, where they remain until late September, October, or even November, after which they disappear until the next year when the whole cycle of events recurs.

MIGRATIONS

It is well known that different shoals of fish appearing in orderly succession in space and time can and do give rise to false appearances of migrations that do not in fact take place.[1] Such phenomena may well underlie, to some slight extent, the changes in the locus of the fishing grounds shown by each of the three fisheries described above. Nevertheless, there can be no doubt that the sequence of events displayed by each of them during its respective season is, in the main, a true reflexion of real and extensive migrations by large bodies of fish.

The almost universally accepted belief has always been that mackerel everywhere, after wintering off-shore, generally in some unknown locality, approach the coasts in spring for the purpose of spawning in shallow water close by the land.[2] The anadromous migration of the large shoals of fish upon which the Newlyn deep-sea fishery depends might appear at first sight fully to conform to this belief; the catadromous migrations of those that support the two other fisheries certainly do not. The fish that are found in the English Channel migrating westward in the opening months of the year disappear offshore, and they do not spawn while in inshore waters. Mackerel eggs are never found in the English Channel in any but insignificantly small numbers and hardly appear at all to the eastward of Lizard Head before about the middle of June.

Close study of the mackerel fisheries in the south-west of England reveals, therefore, that the migrations of the mackerel in the Celtic Sea and English Channel cannot be satisfactorily explained simply by postulating an anadromous spawning migration in the spring of each year and a reverse migration in the late autumn and early winter when mackerel largely disappear from inshore surface waters. Still less will this explanation suffice in the light of the knowledge we now possess that in all this wide region there is only one important spawning ground lying far out to the westward of the English coast. This spawning ground has been surveyed in detail and the results described elsewhere by Steven & Corbin (1939) and more fully by Corbin (1947). From the information contained in those papers a generalized diagram has been prepared (Fig. 5), from which can be seen at a glance the location of this spawning ground and its relation in space to the mackerel movements revealed by the three commercial fisheries described above.

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[1] E.g., the herring in the North Sea.

[2] This is fully discussed on pp. 532–4.

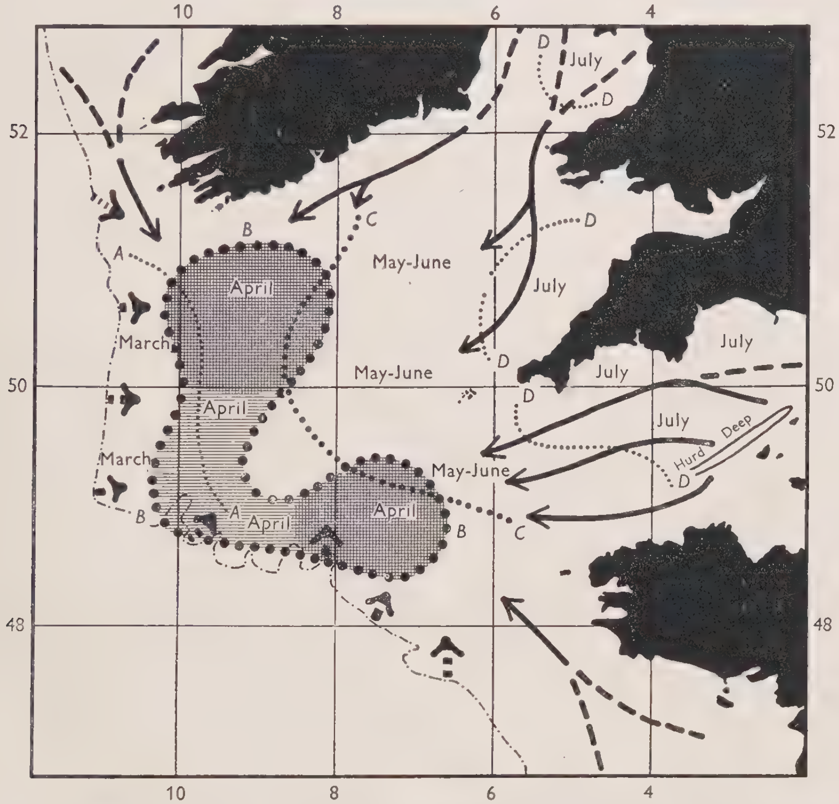

Fig. 5. Generalized diagram indicating the migrations of the mackerel in the English Channel and Celtic Sea in relation to the spawning ground. For further explanation see text, pp. 525–6. ·—·—·—· = 100-fathom contour.

Spawning on a small scale begins as early as March to the westward of the dotted line *A* in Fig. 5—i.e. in the vicinity of the 100-fathom contour which, in that area, closely follows the outer edge of the great continental plateau lying to the south of Ireland. The greatest intensity of spawning takes place in April in the area enclosed by the dotted line *B*. Within this area there are two sub-areas (darkly stippled in Fig. 5) of maximum egg density—one situated from 40 to 100 miles south of Fastnet, and the other from 50 to 80 miles south-west of the Scilly Islands. It will be seen that these two sub-areas are situated opposite and to seaward of the entrances to the Irish Sea and the English Channel. It may well be that they represent two distinct spawning grounds that meet and overlap, and whose boundaries cannot be distinguished where the overlapping takes place.

Spawning continues after April, but with gradually decreasing intensity, for another 3 months or so, the locus of spawning activity moving the while slowly eastwards towards the English coast. In May and June all spawning has ceased to the westward of dotted line *C*. By July such meagre spawning as still continues is residual and unimportant and is confined to the close vicinity of the land—within the confines of the English Channel, Bristol Channel and Cardigan Bay—i.e. to the eastward and landward of dotted lines *D* in Fig. 5. A few eggs are also found at this time in the Irish Sea (Scott, 1913, 1914*a*, *b*).

In so far as the south-western area is concerned, therefore, it is now definitely established that mackerel begin to spawn at least as early as March in the deep and distant waters of the Celtic Sea near the 100-fathom line to the south of Ireland; that spawning activity reaches a highly intensive maximum in April in waters only slightly less distant; and that such spawning as continues into late spring and early summer in shallow inshore waters is residual and unimportant. Those mackerel that approach the south-western shores of England from the westward in early spring have already got rid of most of their eggs before reaching inshore localities. Those that are already present in coastal waters in the opening months of the year do not spawn there but migrate offshore to the common spawning ground of the region before doing so. The apparent anomaly hitherto presented by various bodies of mackerel migrating in different directions at the same time, now becomes resolved, therefore, into the simple picture of various groups of fish migrating from the different places in which they had spent the winter to the common spawning ground of the region.

The various schools of mackerel do not all arrive in the spawning region at the same time. This gives rise to the decided 'spread' of spawning activity in both space and time. Another contributory factor is that in this species the eggs mature in successive batches that are spawned one after another during an extended spawning period. Ripe translucent ova appear in the ovary distributed widely and irregularly amongst the still unripe yellowish ova, producing a peculiar, speckled appearance that for lack of a better term has been called the 'plum pudding' stage. These ripe ova are dehisced into the lumen of the ovary which then, on superficial examination, may show no trace of ripe eggs. Unless opened up such an ovary can be, and often has been, described as 'unripe'. In the mackerel, in fact, a fully ripe ovary is never present; the most that is ever found is an ovary containing some ripe eggs. Cunningham (1889,

p. 25) was therefore in error in thinking that the ovaries and testes of all adult mackerel ripen rapidly and simultaneously and that 'all the reproductive products in a given fish are matured and shed within a short space of time'.

The important question now arises, where do the mackerel come from to this Celtic Sea spawning ground? It seems clear that many, perhaps even the majority, must have been in offshore waters prior to March, since we now know that some of them are already spawning at that time in the vicinity of the 100-fathom line (Fig. 5). Although definite proof is at present still lacking, there is good reason to believe that these fish had come out into deep water during the autumn of the previous year, at the time when they are known to disappear from the surface waters inshore. But where did they spend the ensuing winter? Before providing an answer it is convenient to consider first those other fish which, unlike the majority, do not move outward and westward into deep water in the autumn but spend the winter months on or near the sea bottom in shallower places nearer land—e.g. along the edge of the Hurd Deep some 40 miles south-east to south-south-west of Start Point (Cligny, 1905, 1912; Bullen, 1908), along the southern side of the Vergoyer Bank near Boulogne, and around the numerous small scattered sand banks in the vicinity of Dieppe (Cligny, 1905; Le Gall, 1935). Of the northern fish, numbers sojourn during the winter months on the bottom around the Smalls and Saltees, and are fished from there, particularly by French trawlers (Le Gall, 1928, 1935). At this time these fish are truly demersal and can be caught on the sea floor by commercial trawlers specially equipped for the purpose.

It is not clear what the conditions are that attract the mackerel to certain restricted situations on the sea bed in winter. The only feature that can be detected as common to all of them is an interruption in the level of the sea bed caused by banks or gulleys. There is no uniformity of depth and none of temperature. Mackerel fished along the edge of the Hurd Deep are taken in about 40 fathoms; around the Vergoyer Bank in 12–18 fathoms; in 11–14 fathoms around the Dieppe Banks; and in 30–50 fathoms in the Smalls and Saltees areas. It seems likely that associated with these unevennesses in the sea bed there must be some condition of turbulence—slight perhaps—that is all-important for the mackerel. Although the presence of well-defined mackerel shoals (such as those of the Hurd Deep, Vergoyer Bank and the other localities mentioned) cannot be recorded with absolute precision around the many declivities and acclivities on the floor of the Celtic Sea, mackerel are regularly trawled from various parts of it.

The winter habits of the mackerel, therefore, are now seen to fall into one coherent pattern and the inconsistencies that puzzled earlier writers arose simply through inadequate knowledge. The general statement that the mackerel is a pelagic and migratory fish must be modified. The adult mackerel, at any rate in the English Channel and Celtic Sea, is pelagic and migratory only during a portion of the year. In the other part it is demersal. During the first portion of its demersal period it packs densely in restricted areas and is non-migratory. This was first noted by Cligny (1905, p. 99), who states that these bottom shoals are so dense and so sharply delimited that of two trawlers working side by side one will have a large catch of mackerel and the other none. This is also referred to by Bullen (1908, p. 283), and has been confirmed by old fishermen who participated in some commercially unsuccessful trawling experiments for mackerel from Plymouth.

The fortunes of the fishery reveal that this strongly delimited, densely packed phase of the bottom-living period lasts only for a short time—2 or 3 months at the most. Thereafter the concentration spreads outward in one or more directions from its focal point. In so doing the fish still remain in packs, but of more normal density, the extreme compactness of the first bottom phase having been lost. The Hurd Deep fish, for example, after remaining stationary in a restricted area along its edge until about January, then spread in a north-westerly direction towards Start Point and the Eddystone, where they are caught by French trawlers until the month of March or April.

During the years 1936–39 the Plymouth Laboratory's research ship *Salpa* and a local steam trawler caught 753 mackerel in nine small lots during January–April in an ordinary otter trawl towed very fast on the bottom in the Lizard–Start Point area. The positions of capture (shown as a composite diagram in Fig. 6) of even those few catches indicate a westerly spread of the fish on the sea floor in those early months of the year.

It is during this slow dispersal phase that the change-over from demersal to pelagic habit takes place. Not all at once, but successively, shoal after shoal rises to the surface, and, after they have done so, the spring migration to the spawning ground takes place.

The presence of the Plymouth drift fishery for mackerel off Start Point and the Eddystone in the early months of the year is thus easily understood. The fish that spend the earlier winter months in the vicinity of the Hurd Deep come to the surface in that area and then make their way 'down channel' on a spawning migration to the spawning grounds in the Celtic Sea. Likewise, the fish that winter by the Smalls spread southward across the mouth of the Bristol Channel before rising and continuing their way for some distance parallel to the Cornwall coast and then turn westward to the spawning grounds. On these fish the mackerel drift fishery of the North Cornwall coast in early spring depends. The Saltees fish, and perhaps others that have wintered to the westward of the St George's Channel, spread westward parallel to the Irish coast before rising and turning southward towards the spawning grounds, thus providing the catches close to the Irish coast in the early months of the year (*vide* p. 522).

It seems unlikely that all of the vast mackerel population of the whole south-western area can find room to winter hard by the slopes of the Hurd Deep and the various banks and shoals that have been mentioned. Doubtless some are present also in other inshore places (*vide* Green, 1894, pp. 357–8); but even so, it seems certain that the vast majority must go farther afield to find similarly suitable conditions. This involves a return to the bottom of the Celtic Sea with its numerous banks and knolls, and it is significant that mackerel are regularly caught by British steam trawlers in their vicinity. It may well be that even those slopes also are not sufficient in number and extent to accommodate the whole population and that many fish have to seek the declivity of the continental slope in order to pass the winter in the conditions they require. That mackerel should spend the winter months hard by the outer edge of the continental plateau is entirely consistent with their known habit elsewhere of concentrating where there is an interruption in the level of the sea bed.

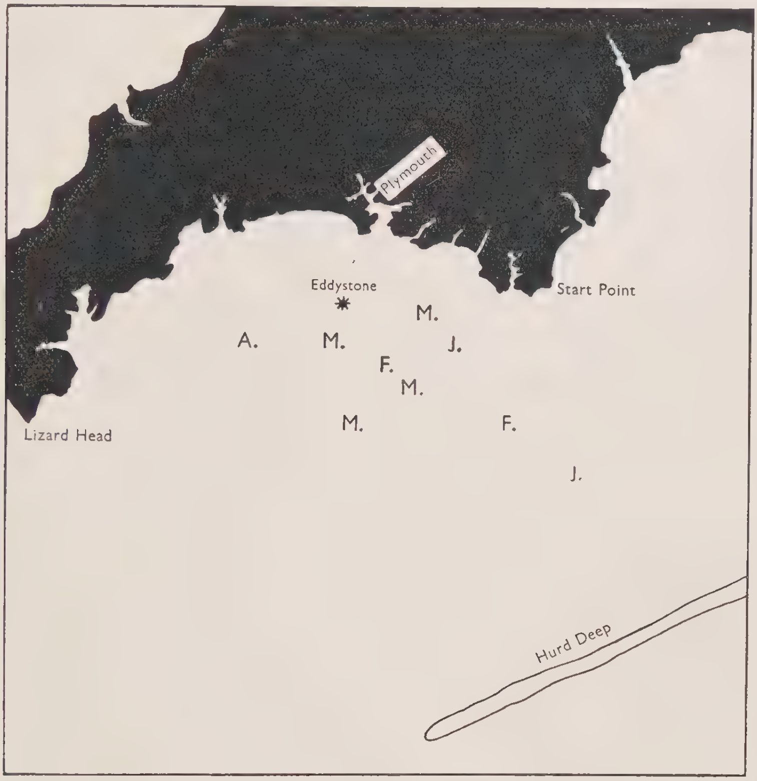

Fig. 6. Chart of area Start Point to Lizard Head. Letters indicate positions in which mackerel were captured on the bottom by two Plymouth vessels during the years 1937–39. J = January; F = February; M = March; A = April.

Although absolute proof is lacking, it appears to be a fully justifiable assumption that these mackerel, acting in conformity with what is now known of their fellows, spread inwards over the outer fringes of the continental plateau in the opening months of the year and then, rising from the sea floor, form part of the great pelagic shoals that migrate eastwards in the Celtic Sea and spawn there in the early spring before continuing their landward journey. In other words, that part of the sea floor from which they approach the spawning ground happens to be to the westward and seaward of it. Other fish, that wintered near other suitable acclivities and declivities nearer the coastlines, approach the spawning grounds from various other directions at the same time. But the directions in which the shoals are moving are merely incidental. The significant point is that they all have wintered in comparable conditions in widely scattered localities, from the Hurd Deep and the Smalls to the edge of the continental slope at the outer boundary of the Celtic Sea; all rise to the surface in spring and migrate to a common spawning ground, thereafter returning shorewards again and dispersing along the coasts during the summer and autumn; and all, or nearly all, return to the sea floor in winter. How far afield they go in their summer migrations it is at present impossible to decide with any degree of certainty, but it is not improbable that some pass through the Straits of Dover to and from the southern North Sea, as suggested by both Allen (1897, p. 28) and Ehrenbaum (1914, p. 51). Others in all probability spread throughout the full extent of the Irish Sea.

The arrowed lines on the chart in Fig. 5 indicate the movements of the various schools of mackerel to the spawning grounds.[1] These are true spawning migrations, and appear to have no relation to food, for the mackerel that rise to the surface waters in the early months of the year undergo a period of fasting, not from 'choice' apparently, but simply because there is very little available food there. They do not fast on the bottom where a certain amount of food is available, and they break their fast afterwards in the upper layers when opportunity offers—as it sometimes does in an otherwise barren sea by the appearance of a shoal of small pelagic fish such as *Maurolicus pennanti*. Amongst samples of mackerel from the Celtic Sea area in early spring, most of which are fasting, it is not unusual to find a few individuals whose stomachs are packed with those small fish, as many as thirteen having been counted in a single stomach.

Of the 753 mackerel caught between 1936 and 1939 on the bottom between Lizard Head and Start Point (p. 528) 67 % contained considerable quantities of food consisting chiefly of small fish and Euphausiids (*Nyctiphanes couchii*).[2] On the other hand, 600 pelagic fish caught by drift net in the Celtic Sea in the months of March[3] during those years contained food in only 43 % of the stomachs and then only in very small quantities, apart from a few individuals that had gorged themselves with *Maurolicus pennanti*.

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[1] Broken lines indicate movements that are as yet presumed and not proved.

[2] One stomach contained seventy-three individuals of this species plus unidentifiable crustacean remains.

[3] No drift net samples were examined in January and February.

Over the course of one full year, therefore, the life of most adult mackerel in the south-west region appears to fall into two main periods, a demersal period and a pelagic period, with a brief transition period during which the fish return to the bottom and reform shoal.[1] This can conveniently be summarized as follows:

1. DEMERSAL PERIOD

(i) *Compact phase*

Intensely dense and extremely circumscribed concentrations of fish massed on the sea floor in very localized positions distributed over wide areas.

November, December

(ii) *Deployment phase*

Concentration diminishes; still keeping to the bottom the fish spread slowly outwards over adjacent areas before ascending to the upper waters and giving rise to pelagic shoals.

December, January, February

2. PELAGIC PERIOD

(iii) *Shoaling phase*

Active migration of the shoals to the spawning grounds and return (or continuation) shorewards.

January–July

(iv) *Dispersal phase*

Shoals broken up and fish dispersed in inshore waters around all coasts.

June–October

3. TRANSITION PERIOD

(v) *Reconcentration phase*

Disappearance from surface waters and return to phase (i).

October, November

During phase (ii)—the deployment phase—the fish appear to perform small diurnal vertical movements, rising from the sea floor during the night and descending again during the day. Trawling during this phase is therefore most successful during daylight hours (Bullen, 1908, p. 283).

DISCUSSION

In the light of this new information concerning the habits and migrations of adult mackerel in the south-western region it is instructive now to examine what is known of their movements and behaviour in other places.

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[1] These changes do not take place everywhere simultaneously, so there is no period of the year during which at least a few scattered schools of pelagic mackerel cannot be found.

With regard to mackerel in all the European seas Allen (1897, p. 25) makes the general and comprehensive statement that 'the first approach of the mackerel to the coast in spring or early summer is for the purpose of spawning' and adds the interesting comment that 'the advantage to the species of the young fish being hatched out near the shore where the smaller forms of pelagic organisms are present in abundance and the plankton is increased by the numerous larval forms of those species which inhabit coastal waters, is obvious'.

With special reference to the Celtic Sea and the English Channel area Allen (1897, pp. 12, 17) mentions the presence of fish 30–40 miles from land between Start Point and Plymouth in the months of January to March, at the same time giving the end of March or early April as the time of the approach of the main shoals 'towards the southwest coasts of Ireland and the west coast of France'. He makes no attempt to explain the presence of mackerel so far up channel in winter and early spring while the main shoals are still far away to the westward. Ehrenbaum (1914, p. 13) also states that the great majority of English Channel mackerel appear to arrive in early spring from the adjacent waters of the Atlantic. He attempts to explain the presence of mackerel far up the channel long before the main shoals arrive by suggesting that 'the mackerel sometimes move, in great numbers, still keeping to deep water, far eastward, into the Channel', before rising to the surface. This author, too, believed that mackerel everywhere move in towards the coasts in spring to spawn (1914, p. 17) and gives the months of May, June and July as 'the true spawning time' in both European and North American waters. Much emphasis is placed upon this uniformity of spawning in such widely distant regions. Only in the Mediterranean is the spawning time stated to be 2 months earlier. In a footnote Ehrenbaum (1914, p. 75) makes only passing reference to an important statement by Rathbun, quoting Hardin (1896, p. 81) who found in the New York market mackerel taken on the 17 April some 65 miles south-east of Cape Henry, that were already spent. This observation is possibly of much more importance than Ehrenbaum attaches to it and may indicate much earlier spawning than has been ascribed to mackerel in those waters (cf. p. 535, *infra*).

Meek (1916, p. 320), also in a general statement embracing all mackerel (*Scomber scombrus*), says that 'the spawning migration is an anadromous one', that the season is May to July, and that spawning takes place when they arrive in coastal water (*op. cit.*, p. 326).

Although, as we now know, these general statements concerning the mackerel do not hold good in the English Channel and Celtic Sea, it is significant that, in the North Sea, they are partly true. In that area by far the largest number of mackerel eggs have always been found on the Norwegian side of the Skagerrak very close to the south coast of Norway (Ehrenbaum, 1914, p. 18), and at its inner end off the Swedish coast from Väderöfjord to Hallö and Paternoster 'and thence diagonally across to the Skaw' (Ehrenbaum, 1923, p. 11). Here, without doubt, is a shoreward migration to spawn, chiefly in the months of May, June and July. But it should be noted, by reference to a chart of the eastern North Sea, that *although the migration is shoreward from adjacent offshore waters, it is at the same time a migration from shallower water to the vicinity of the* 100-*fathom contour*.

There is thus a very close similarity between what we now know to be the chief spawning locality of the south-western region and that of the North Sea area. Both lie close to the 100-fathom line. In both areas this contour closely follows the edge of a well-marked slope in the sea bed from shallow to deep water—i.e. to the depth of the Atlantic Ocean in the Celtic Sea; and, in the Skagerrak, to the lesser but, nevertheless, considerable depths (over 400 fathoms) that are present there and which are not found anywhere else in all the North Sea region.

There is the further similarity that mackerel eggs are found, but in much smaller numbers, widely distributed over adjacent parts of the North Sea and the Kattegat (Buchanan-Wollaston, 1911, p. 218). Ehrenbaum has shown that in the North Sea, too, during the colder season of the year, from November till about May, great numbers of mackerel are present on the bottom chiefly around the Great Fisher Bank and northwards to the Viking Bank along the edge of the Norwegian Channel (1912, p. 4; 1914, p. 36). He also points out that the trawl catches of these fish over the different months of the year 'seem to indicate that the mackerel taken in winter are for the most part identical with the shoals which in spring appear on the coasts of the North Sea and Skagerrak in order to spawn' (1914, p. 36).

What we now find, therefore, is that after spending the winter months on the sea floor in the vicinity of the slopes produced by banks and gulleys, the mackerel in both the North Sea and south-western areas migrate to certain restricted spawning grounds in the vicinity of the 100-fathom line. It so happens that in the North Sea this contour lies close to the Norwegian and Swedish shores. This brings about the anomalous result that mackerel migrating from the shallow waters of the North Sea to spawn in the deep waters of the Skagerrak, and, to a lesser extent, in other Norwegian Fjords farther north, are, nevertheless, at the same time also migrating shorewards. That is to say, that most of the mackerel in the North Sea, like their brethren in the English Channel and Celtic Sea, migrate from their winter quarters to deep water to spawn; that in the North Sea this deep water happens to lie close in by the shore whereas in the south-western region it lies far out in the Celtic Sea, a long way from the land.

It is this apparent anomaly that hitherto has led to such confusion in trying to interpret the migrations of the mackerel. The coincidence that the deep water they favour happens, in the North Sea, to lie hard by the land, and that this was the first spawning ground to be investigated has given rise to the belief that all mackerel migrate shorewards to spawn. The fact that mackerel eggs are never found except in comparatively small numbers near the shore around the south and west coasts of England should have led to at least a suspicion that this did not hold good there. But with only one remarkable exception this suspicion seems never to have arisen in anyone's mind. The exception was a very enlightened fisherman, Matthias Dunn of Mevagissey, Cornwall, who, in 1893 (p. 3), stated quite definitely that the spawning grounds of the mackerel in the south-west region 'are in those waters covering the plateau of ground within the two-hundred-mile limit of our western and south-western shores, known to our sailors as about or within soundings'. This remarkably accurate statement is not even mentioned, so far as I can ascertain, by any subsequent investigators. Perhaps they had never come across it; or perhaps (more likely) they considered it to be too preposterous for serious consideration. Day (1880–84, p. 85), however, appears to have retained an open mind on the subject, for he says that at certain seasons mackerel approach the shores in countless multitudes 'either prior to, during, or after breeding'.

Respecting the migrations of the mackerel on the western side of the North Atlantic there existed for a long time two very well-defined schools of thought. One held that the mackerel undertook extended migrations both to and from deep water well offshore, and also along the shore, when this was reached, in a south to north direction (Brown Goode, 1879, p. 63). Other investigators and observers (quoted by Brown Goode, 1879, pp. 56 *et seq.*)[1] held that the mackerel spent the winter on the sea floor, not very far from their summer haunts, where they lay in a comatose state either on or even partly embedded in the bottom mud or sand. These apparently opposing views were, in fact, held by American and Canadian workers respectively and were fiercely debated in a controversy concerning American rights to fish in Canadian waters. The American argument was that, since the shoals moved northward from American to Canadian waters, American fishermen were entitled to follow them thither. The Canadians held that, on the contrary, such migrations did not take place and opposed the American claim to a right to fish in their waters.

Each side provided some useful evidence in support of its claim. The American view was supported by the northward movement of the fishery. Canada depended mainly on rather fanciful 'eye-witness accounts' of mackerel being seen on the bottom in a torpid state in winter months, and on the more reliable fact that mackerel occasionally could be caught by nets on the bottom near the shore in winter. Brown Goode himself (1884, p. 102) more or less admits the claim that mackerel are not infrequently found in the stomachs of cod and halibut taken on and near the bottom on George's Banks in the winter season, and Collins (1883, p. 274) reported that in late February, 1882, many mackerel were taken in the stomachs of cod that had been caught near bottom some 10 miles off Egg Harbour, N.J., in 12–15 fathoms of water. Summing up, Brown Goode conceded rather grudgingly that 'it is by no means demonstrated that certain schools of mackerel do not remain throughout the year in waters adjacent to the coasts of Canada' (1884, p. 96). Nevertheless, he considered such cases to be quite exceptional and held firmly to the conviction that the weight of available evidence was overwhelmingly in favour of those who held that the mackerel make extensive migrations along the coasts, in addition to returning to deeper parts of the ocean on the approach of winter.

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[1] The very early Canadian publications by W. F. Whitcher and Henry Youle Hind have not been available to me for direct consultation.

As more information became available, however, the views of both parties became so modified that Bigelow (1925, p. 192) was able to state that 'scientific opinion has gradually crystallized to the effect that the essential features of the seasonal migrations of the mackerel are essentially a spawning journey inshore and into shallow water in spring alternating with an offshore movement combined with a descent into deep water in autumn'. He then adds that, according to geographic conditions, these 'fundamental changes of situation' are accompanied by horizontal journeys of greater or less length and in various directions. According to this author (1925, p. 206) mackerel spawn off the North American coast from the latitude of Cape Hatteras (35° 15′ N.) to the Gulf of St Lawrence, where the heaviest spawning along the whole coastline takes place, closely followed by the Gulf of Maine, especially in the Massachusetts Bay area. In the latter region the chief spawning season is said to extend over the last half of May and the month of June; in the Gulf of St Lawrence spawning activity reaches its maximum a month later in the latter half of June and the first two weeks of July.

Although exact comparisons are impossible because of the different methods and gear used for collection, it may be significant that the records of mackerel eggs obtained in both those regions (Bigelow, 1925, p. 206; Dannevig, 1918, p. 8; Sparks, 1929, pp. 445–450) reveal widespread distribution of eggs in comparatively shallow coastwise waters in numbers that appear to be comparable with those obtained by Corbin in the Celtic Sea to landward of the main spawning centres after maximum spawning intensity had passed. If this indeed be so, much importance must be attached to Bigelow's further statement (1925, p. 207) that, in the Gulf of Maine region, egg records from offshore localities, though extremely scanty, nevertheless clearly indicate that spawning takes place in the vicinity of some or all of the many banks that lie well offshore and over deep water[1] as well as in the shallow coastwise waters of the inner parts of the Gulf.

The evidence so far available, therefore, appears to point very strongly to the probability that the habits and migrations of the mackerel on the western side of the North Atlantic will, on further investigation, be found to be very similar to those of their European kin around the south-west of England and in the North Sea. The existence of hitherto undiscovered, restricted spawning centres of high spawning intensity, probably in the vicinity of the 100-fathom line perhaps as early as April in both the Gulf of Maine and the Gulf of St Lawrence, seems highly probable; and examination of the charts of the two regions suggests that they are well suited to the needs of the mackerel as revealed by our recent researches in the English Channel and Celtic Sea.

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[1] Bigelow appears here to be referring to depths of less than about 180 fathoms, the deepest soundings found in the various deeps and basins of the Gulf of Maine which is the oceanic bight between Cape Cod and Cape Sable. He adds (1925, p. 209) that 'there is no reason to suppose that they ever breed outside the continental slope', the edge of which, in that region, follows more or less closely the 200-fathom contour.

Although the migrations of the adult mackerel in the English Channel and Celtic Sea have now become clear, the migrations of the young and immature fish are still obscure, but mention must be made of what little we do know concerning them. Corbin (1947, pp. 73–76) has shown that the larval and post-larval stages, as would be expected, are numerous on the spawning grounds for a short time after the eggs have hatched out; thereafter, they disappear from catches and little is known concerning them. During our investigations the largest post-larva captured in these waters was 21 mm. in length caught in the month of June.

But small mackerel, of from about 13 to about 17 cm. in length, appear in some years in bays, harbours, and estuaries around the south-western shores of England for a short period in early autumn. In 1926 small fish appeared in Plymouth Sound in August and several were caught in sprat nets, their size ranging from 13·0 to 17·2 cm. in length (mean length of all fish 15·3 cm.). In 1927 small mackerel again appeared in the bays and estuaries around the Devon and Cornwall coasts. Fifty of them caught in a sprat seine during August had a mean length of 13·6 cm., the total range being 12·5–15·2 cm. In 1937, 273 small mackerel caught at Newlyn on 4, 6, and 7 August had a length range of 8·0–16·4 cm. with a mean length of 12·7 cm. Those fish first appeared in the middle of July and remained inshore until nearly the end of September. They were present in very large numbers—so much so that reports of their presence in such abundance were at first disbelieved. Many Newlyn fishermen were very definite in their assertions that they had never seen mackerel of such small size before.

Their appearance, in fact, in inshore waters in this region, takes place only at long and irregular intervals. Nor are they found with any greater frequency elsewhere in British waters. The Scottish Fishery Board[1] records the capture of small mackerel on the bottom in a small-meshed covering of the cod end of an otter trawl in September and November 1929; September and October 1930; September and October 1932; August, September and October 1933; August 1935; and in September 1936.

There are no records in the Board's log-books of any catches of these small sizes in 1927, 1928, 1931, 1934 and 1937.

The capture of small mackerel is not to be expected in an uncovered trawl, but Hickling,[1] while fishing for hake off the west coast of Ireland, has come across them in the stomachs of hake and certain other fishes. Ehrenbaum

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[1] Private communication.

(1923, pp. 19 *et seq.*) gives details of the capture of small mackerel in the North Sea by several workers of different nationalities in the late summer and autumn. Malm (1877, p. 409) mentions a great shoal of small mackerel that appeared in the Skagerrak, near Christenburg in the Gullmarfjord, on 27 July 1872. They were so small that they all escaped through the meshes of ordinary seines and only ten could be obtained for examination. These fish were between 67 and 100 mm. in length. To the fishermen of the district such small mackerel had until then been entirely unknown so that, as on the Channel coast of England, they must arrive only on rare occasions at long intervals.

From the information available, therefore, meagre and incomplete though it be, it is evident that juvenile mackerel, like the adults, are present at times on the sea floor and at other times in the upper layers of the sea. Their appearance in some years in huge numbers in inshore waters for a few weeks in summer and early autumn reveals that they also carry out migrations, but the fact that they do not appear around the shores every year suggests that those migrations, in the main, are less extensive and less regular than those of the adult fish.

One cannot but conclude, therefore, that the migratory behaviour of young mackerel may be very similar to that of the adults; that they seek bottom in the late autumn and winter and rise again to the upper layers in due season. As they so seldom come inshore, it would appear that their horizontal migrations are, as a rule, less extensive than those of adult fish. As they grow and approach maturity, those migrations must approximate more and more closely to those of the adults until at last, when they reach maturity, they join the spawning shoals and migrate with them.

SUMMARY

In the English Channel and Celtic Sea mackerel spend the winter months on the sea floor densely packed in places where its level is interrupted by banks and gulleys.

In the early spring the fish rise to the surface and migrate to a common spawning ground that lies far out to the westward of the Scilly Islands in the vicinity of the 100-fathom contour.

The very localized positions in which mackerel spend the winter are widely distributed throughout the area in both deep and shallow water. Large schools of migrating fish converge upon the spawning ground from many directions, therefore, in the spring for spawning.

Fish that have wintered near the land must migrate *offshore* to reach the spawning ground; those that spend the winter on the bottom to seaward of the spawning ground must migrate *shorewards* to reach it. Off the south-west of England there is no single shoreward migration to spawn in shallow water as has previously been thought.

In the North Sea the chief spawning grounds of the mackerel are also near the 100-fathom contour which, in that region, happens to lie very close to the land

in the Skagerrak and along the Norwegian coast. The chief spawning migration of the North Sea mackerel is therefore towards the coast from offshore localities. This migration is, at the same time, chiefly from shallow to deeper water.

Existing information concerning the mackerel populations on the western side of the North Atlantic points to the probability that their spawning habits and migratory movements do not differ greatly from those of the mackerel in North European waters.

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THE LARVAL DEVELOPMENT OF *OPHELIA BICORNIS* SAVIGNY

By Douglas P. Wilson, M.Sc., F.R.P.S.
Zoologist at the Plymouth Laboratory

(Text-figs. 1, 2)

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INTRODUCTION

The development of the Opheliidae has hitherto been unknown. Eggs and sperm have previously been described, but the larvae have not. The most recent attempt to study the development was made by Brown (1938) at Millport, using the small species *Ophelia cluthensis* McGuire, which is abundant in the sand at a certain level in Kames Bay. He described the eggs and sperm, and obtained cleavage as far as the 4-cell stage. McGuire (1935) had previously also observed cell division up to the 4-cell stage in the same species. Many years previously Bullot (1904) did experiments on artificial parthenogenesis in an *Ophelia* and obtained swimming larvae, but did not figure or describe them in detail. Benham (1896), in a text-book, stated that the eggs of *Ophelia* are enclosed in a jelly, but it is not clear whence this statement derives.

The Opheliidae are a family of small worms, most of them burrowing in sand or mud. The distribution of the various species seems to be rather markedly localized and most species appear to inhabit only a fairly narrow range in grade of bottom soil. It seemed likely that the development might be of special interest, especially the settling reactions of the larvae. This has, on the whole, proved to be true. In this present paper the larvae are described; the experiments on settling reactions will be discussed separately.

I am glad to have this opportunity of thanking Mr N. A. Holme of Exmouth, who drew my attention to the possibility of collecting *O. bicornis* Savigny on the sand banks at the mouth of the Exe estuary. The species had been found there many years earlier by Allen & Todd (1902), but has not attracted particular attention in that locality since. Mr Holme on several occasions specially collected worms for me and forwarded them to Plymouth. At other times I collected them there myself.

METHOD

O. bicornis Savigny lives in the loose clean sand of the Bullhill Bank and of the Polesands at the mouth of the Exe estuary. I myself have collected them only on the Bullhill Bank, but Mr Holme has also visited the Polesands and found them there, also in lesser abundance in other parts of the estuary. He will subsequently be publishing an account of the fauna of the Exe estuary, and will deal with their recent distribution in detail. Here it is sufficient to say that they are most abundant about the half-tide level, which approximately coincides with the top of the Bullhill Bank.

The sand in which they live is thus uncovered for several hours each tide. They inhabit the top few inches and are easily turned up with a spade or a trowel, and can even be got by using the fingers alone, drawing them through the sand. The adult worms are a little over an inch long; mature males are white or pale cream, mature females a deep metallic green. Immature and spawned worms are pinkish. All have a beautiful iridescent sheen. In collecting they were put into large jars with quantities of sand, and in the laboratory were kept under sea-water circulation in bowls with plenty of their natural sand to burrow in. Some rough experiments indicated that they survive better when the water is drained away for several hours each day to simulate the tides of their normal environment. They could be kept up to a fortnight or three weeks, but the best fertilizations were made the day they were collected, or within a few days afterwards.

Artificial fertilizations were made by slitting open the worms, care being taken to avoid contamination with much blood. Several times, however, worms spawned naturally in the bowls and larvae from naturally spawned and fertilized eggs were found to be on the whole more virile than those from artificial fertilizations. Worms shedding eggs or sperm protruded the head and anterior segments from the sand; sometimes as much as half the body was exposed, particularly by the females; the males might show only the head and first few segments. The eggs and sperms issued from out of the hole from which the front end of the worm protruded; it was not possible to see them coming out of the body of the worm. The eggs and sperm were often ejected in 'puffs' caused by a sudden contraction of the worm into its hole. When worms in the act of spawning were removed in a dish to a microscope stage the spawning ceased and did not again start. After spawning, the hole of a female would often be surrounded by eggs loosely piled around its mouth; they were not adherent to one another; in nature the eggs would be swept away by the tidal current.

Developing eggs were kept in finger bowls, no more than sufficient to cover the bottom in a single layer being put into any one bowl. As soon as a goodly number of larvae had swum to the surface they were decanted off into a clean bowl and there reared. No food was needed, but the bowls were covered with sheets of glass and tissue paper to keep out dust and excess light. Bowls placed near the sea-water circulation remained fairly cool in hot weather, with benefit to the larvae. At about the time of metamorphosis a little food in the form of small autotrophic flagellates and the diatom *Nitzschia* was provided.

Larvae were examined and drawn alive, scale being obtained by the use of a squared-net micrometer in the eyepiece, the preliminary drawing being made on squared paper. Bristles were drawn with a camera lucida.

ACCOUNT OF THE DEVELOPMENT

Ripe eggs are dark green or greenish brown in colour. When freshly obtained from the female by slitting the body wall they are generally oval plates (Fig. 1 *a*), about 150 μ long by 130 μ broad, with a clear germinal vesicle near the centre. When seen in side view (Fig. 1 *b*) there is a definite bulge in the region of the nucleus. Sometimes a nucleolus is present, sometimes it has already disappeared. The cytoplasm is thinned out at one end, giving a clearer region when viewed with transmitted light. The rim round this region is, however, thicker. The egg is closely invested in a well-defined membrane outside which there is a completely transparent and invisible jelly, several microns thick, which makes it impossible to push one egg into visible contact with another.

If the eggs are not fertilized, there is no change in their appearance. They can remain in this condition for many hours (overnight) and still be fertilizable, though they seem to give healthier larvae if fertilized immediately.

Eggs spawned naturally and examined at once have also been found to correspond closely with this condition. Usually, however, such eggs are fertilized at once by males shedding sperm in the same bowl, and quickly proceed to develop.

From a female which had been interrupted in her spawning I have obtained, by slitting the body wall (a few hours later), eggs which were not quite the same. They were oval disks with a germinal vesicle and a bulge (when viewed laterally) in the region of the nucleus, but there was no specially thinned-out area at one end, and one pole was flattened as though for the reception of the sperm. Some of these eggs were kept for some time, but underwent no further change; others were fertilized and proceeded to develop, but on the whole did not give such healthy larvae as eggs of the other sort.

Some other variants of egg shape have been noted, so that at the moment it is not quite certain which should be regarded as the normal recently spawned but unfertilized egg.

On fertilization the egg rounds up, becoming spherical, of smaller diameter (about 95 μ) than that of the disk-shaped unfertilized egg and more opaque. The egg-membrane rises off the surface of the egg in a crumpled manner (Fig. 1, *c*) and at the same time the invisible jelly-layer outside swells up. This is revealed by the excess sperms caught in it to form a halo around the egg, and by the greater distance eggs are kept apart from one another when attempts are made to push them into contact. The thickness of this jelly is about equal to the diameter of the egg itself.

Whilst the eggs are rounding up, the germinal vesicle disappears and polar bodies are soon given off; they are clearly visible under the egg membranes. This is followed by the first division stages.

In 24 hours or less, according to the temperature, larvae swim actively up to the surface and gather in swarms round the side of the bowl. They are not phototropic. They are almost spherical (Fig. 1, *d*), rather opaque, and the same greenish brown colour as the eggs. Cell limits are fairly distinct, the cells being relatively large and densely granular. The central mass of the developing gut is rather more opaque and darker than the cells forming the body wall. The blastocoel is almost entirely occluded. A stomodaeal invagination is present. The whole is enclosed in the egg- or fertilization-membrane through which the cilia project. There is a long apical tuft, and a prototroch forms a complete band round the equator. The individual prototrochal cells can be traced fairly clearly—there is a double row, the cilia of the posterior row being a little shorter than those of the anterior. There is no telotroch. The larva swims forward in the direction of the apical tuft, mainly on a horizontal axis rotating as it goes.

As growth proceeds the larva elongates, the widest region of the body being at the prototroch. The apical tuft is large, the cilia varying in length, the longest in the middle. The prototroch is a broad uninterrupted band, immediately behind it ventrally is the developing stomodaeum. A telotroch of relatively short weak cilia soon appears (Fig. 1, *e*); it is interrupted ventrally and dorsally by median gaps. Some patches of neurotrochal cilia appear and there is a long very thin cilium at the extreme posterior end. Granular greenish patches (chromatophores) form on the head in a transverse row immediately behind the prototroch, and a few smaller ones just in front of the telotroch.

With further elongation the first trunk segments become discernible through the segmental arrangement of additional chromatophores on the trunk (Fig. 1, *f*). Chromatophores also appear on the pygidium. On about the third day a granular reddish brown eyespot develops on the right side. The larval cuticle thickens over the head. It can be seen that the prototroch consists of three or four moderately distinct transverse bands of cilia placed very close together. The cells of the prototroch are more opaque than are those of the rest of the body wall—a feature that persists as long as the prototroch is present. The tissues generally are very granular and rather opaque, especially gut tissues not indicated in the drawing. The neurotroch, consisting of several patches of short cilia, becomes more strongly marked; it ends posteriorly in the mid-ventral gap in the telotroch. The anus is already formed. As further structures differentiate (Fig. 1, *g*, *h*, *i*), the diameter of the prototroch shortens, the larva acquiring a more elongate appearance without any real gain in length. Segmental grooves appear, and parapodial lobes arise as small swellings on what will be the first two setigers. The first bristles soon protrude just dorsal to these lobes. The anus opens immediately behind the dorsal gap of the telotroch, and first one and then two pairs of papillae appear at the extreme posterior end of the body. The ventral pair of these is larger than the dorsal. There are now two eyespots and sometimes a third on the right side. The eyespots are cup-shaped, the opening of the cup being directed ventrally and laterally.

The larva can now wriggle violently, indicating the development of trunk musculature. The larva is a little more transparent than previously, the prototroch being the most opaque area. It should be noted that the line drawings give but a poor representation of the texture of the tissues. The gut is probably open at both ends, but it is uncertain whether the larva is feeding or not. The gut is still fairly granular. The mouth is well ciliated and there are short cilia on each side of it. The proboscis is developing.

The trunk now slowly elongates (Fig. 1, *j*) whilst the diameter of the prototroch remains more or less the same. The parapodial lobes of the third setiger appear (Fig. 1, *j* and Fig. 2, *a*, *b*), but not for some time does this segment acquire bristles (Fig. 2, *c*). The bristles of the first two setigers grow longer and are followed by others. First each dorsal bundle acquires a second bristle (Fig. 1, *j*) and later the first setiger gets a ventral bristle on each side (Fig. 2, *a*, *b*), followed later by the second setiger. By the time the third setiger has a single dorsal bristle on each side the first had often three dorsal and two ventral (Fig. 2, *c*) to each parapodium. There is variation in the rate at which the bristles of the first and second setiger appear in relation to the time of appearance of bristles on the third setiger. For a description of the bristles see p. 548.

With further growth the apical tuft loses some of its cilia. The prototroch becomes a little narrower (Fig. 2, *a*, *b*, *c*); it can be seen to be composed of three or four rows of cells. The neurotroch consists of a series of patches of cilia, generally two per segment with considerable non-ciliated gaps between. The larvae swim steadily, sometimes swiftly, forward, rotating slowly, often in a more or less spiral path. Unless moving up or down they swim with the body horizontal, or nearly so.

When the third setiger bristles are seen the larvae are six to eight days old, though sometimes younger and sometimes older according to the temperature. It is at about this stage that metamorphosis first becomes possible, though, as will be shown later, it rarely takes place except in sand of a suitable character. At about this stage too there is a change in the behaviour of the larvae. Whereas during the first few days they had swum up towards the surface and had shown no reaction to light, they now move away from a light source and can be driven to and fro, up or down in the glass bowl by moving an electric lamp into appropriate positions. They gather on the side of the bowl away from the window. At this same stage they are also to a large extent positively geotropic. Thus, if a bowl of larvae be stirred so that they are evenly distributed throughout, and a light-tight cover be placed over the bowl for a few minutes, it will be found that the great majority of the larvae go to the bottom. In a bowl left in darkness all night, however, the majority were at the surface in the morning, these larvae immediately moved away from the light when they were uncovered and gathered about half-way down the bowl on the side away from the window. The cover was replaced for 15 min. at the end of which period the larvae had gathered on the bottom of the bowl.

Negative phototropism and positive geotropism will in the sea lead metamorphosis-ripe larvae to the sea bottom. What happens to them there will be discussed in another paper; we are here concerned only with general details of the metamorphosis.

When ready to metamorphose *Ophelia* larvae readily cling to any solid object with which they may come into contact. The sides of a bowl, the walls of a pipette, and grains of sand are only some of the objects adhered to. They may show this habit as early as the fifth or sixth day. Attachment is effected primarily by the four anal papillae, aided often, especially in older larvae, by the parapodial lobes. Adhesion is effected by a secretion produced by glands at the bases of the papillae and of the lobes, and discharged by canals opening at pores on the tips of these protuberances. Parapodial lobes have one gland for each, but each anal papilla has several. At first, larvae can easily detach themselves and swim away, but after a few days they stick more firmly and this, combined with a loss of swimming strength due to a decrease in power of the prototroch with age, results in their being unable to get away. Thus they become stuck to the glass of a clean finger bowl, though they may be detached by squirting water from a pipette.

A larva attached by the anal papillae to the bottom of a glass dish stands upright with the prototroch beating strongly. It similarly stands upright on sand grains, unless it actually burrows into the sand and metamorphoses. This ability to cling strongly to sand grains must aid the larvae in settling on the current-swept sand banks in which they will live when adult. Such a mechanism seems to be needed in order that they may anchor themselves immediately contact is made with the bottom soil. A quick efficient attachment mechanism is a necessity for settling in regions swept by strong currents, and the anal papillae and parapodial lobes, with their associated glands, fulfil this need.

Larvae, after settling on the surface of the sand, make their way into it. If the sand be suitable, they may stay there, but they have been seen to come out and swim away. Often they remain on the surface of an unsuitable sand, attached to a grain by the anal papillae, the body upright, swaying, with the prototroch beating strongly. It has seemed as if they needed a current of water to launch them up and away from the bottom.

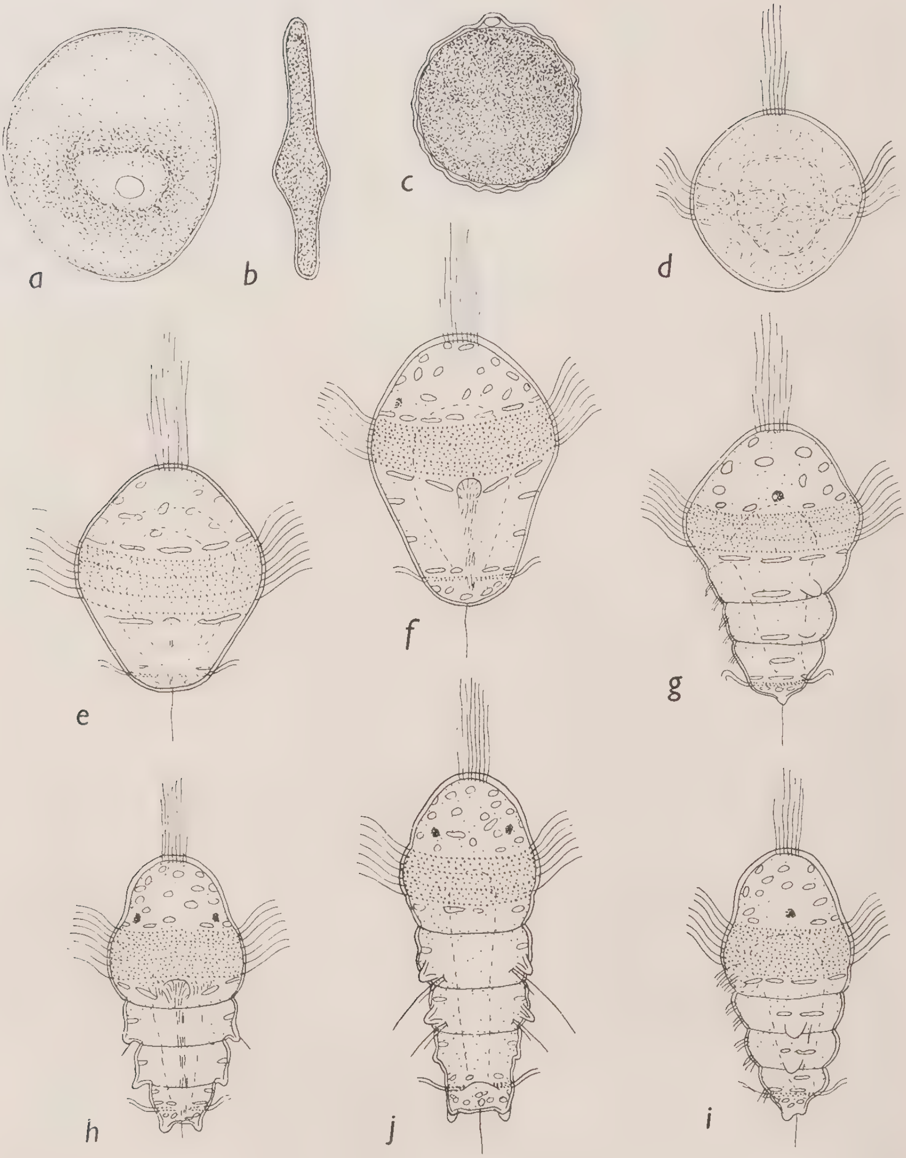

Fig. 1. Eggs and larvae of *Ophelia bicornis*, × 225. *a*, unfertilized egg; *b*, the same in side view; *c*, fertilized egg with polar body; *d*, 1-day-old larva; *e*, 2-day-old larva, ventral view; *f*, 3-day-old larva, ventral view; *g*, 4-day-old larva, view of left side; *h*, *i*, 4 to 5-day-old larva, ventral view and view of left side; *j*, 5-day-old larva, dorsal view.

In a suitable sand the larvae metamorphose. The apical cilia are lost, the prototroch, telotroch and neurotroch disappear and all power of swimming is lost. The body elongates and the worm (Fig. 2, *d*) crawls among the sand grains to which it can adhere strongly. The bristles grow rapidly, especially those of the third setiger which soon exceed in length the anterior ones.

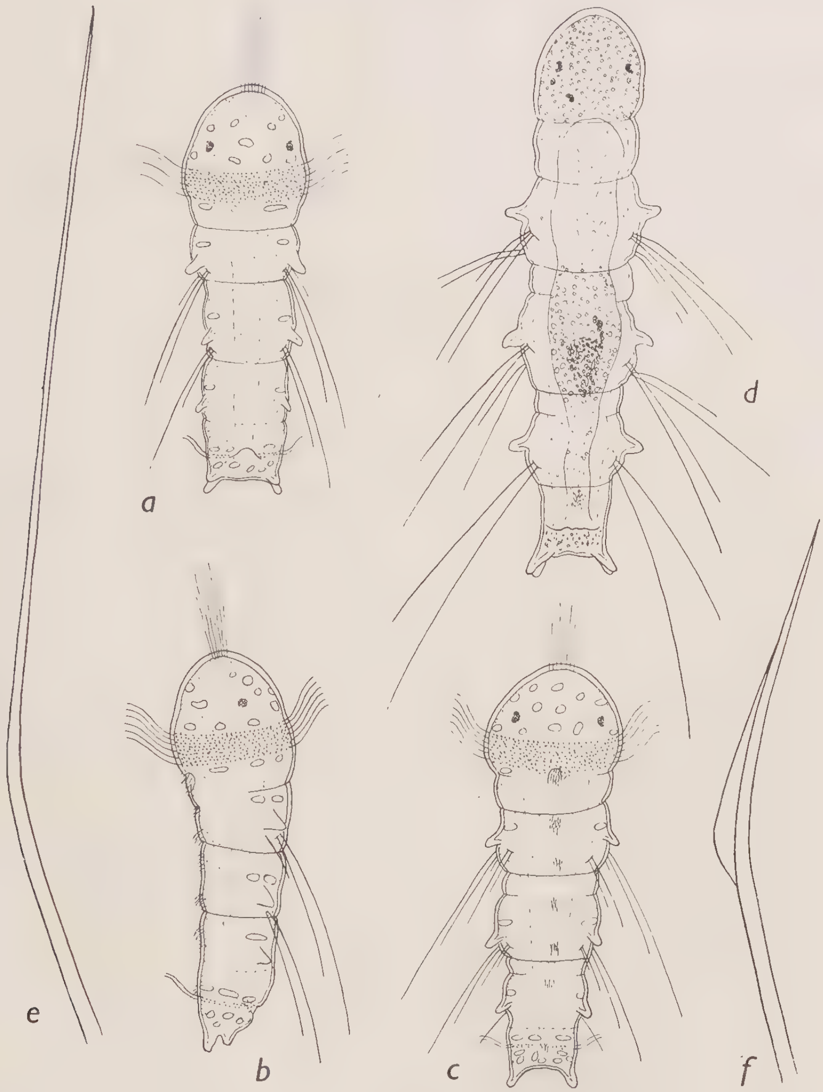

Fig. 2. Larvae of *Ophelia bicornis*, ×225; bristles, ×1600. *a*, *b*, 7-day-old larva, ventral view and view of left side; *c*, 11-day-old larva, ventral view; *d*, young worm, after metamorphosis and 19 days old, dorsal view; *e*, capillary bristle; *f*, winged bristle.

The bristles appear at first sight to be all fine smooth capillaries, often bent at a slight angle near the base (Fig. 2, *e*); more careful observations, however, show that a few are provided with a narrow bordering wing, widest at the bend and narrowing towards the tip of the bristle (Fig. 2, *f*). In living specimens I have recorded as winged bristles the third notopodial in the first setiger, and the two neuropodial of the first setiger, also the shorter ventral of the second neuropodium. In preserved specimens I have not been able to detect a wing on all these bristles, nor even on any bristles of some specimens, though others show it distinctly. Whether this is due to preservation and the factors concerned in mounting and viewing the specimen is not clear, it may be that the presence or absence is a variable feature. The Opheliidae are noteworthy for the presence in the adult of capillary bristles only, so that the presence of even an indication of a wing on larval bristles is an interesting feature, though at the moment its significance is far from clear.

Behind each of the first two eyes a ciliated pit, the nuchal organ, can be seen. A third eye situated more dorsally than the others and behind them, appears on the left side of the head. The head tissues are granular, but the body wall is in general very transparent, revealing the gut. The latter has a ciliated oesophagus, granular stomach in which bottom-living diatoms are visible, followed by an intestine and ciliated rectum which opens at a dorsally situated anus. In lateral view the infolded proboscis, or buccal mass, is a conspicuous feature lying just inside the mouth and under the oesophagus.

The disappearance of the intervening prototrochal tissues has allowed the prostomium to fuse directly with the peristomium, there being a well-marked groove between them. The chromatophores of the head give a darker appearance to that region of the body and this is repeated to some extent at the posterior extremity. The cuticle of the trunk segments is transversely wrinkled as it is in the adult.

No further stages have been obtained by rearing, although young worms have been kept for a few weeks after metamorphosis. They have gradually become unhealthy and died, presumably because in dishes it has not been possible to reproduce the conditions they would find in their natural environment, especially as regards food supply.

At the end of October 1947, a visit to the Bullhill Bank produced two young *Ophelia*, which almost certainly represented the brood of the previous summer. They were obtained by sifting the sand through a fine meshed sieve and examining the washing under a dissecting binocular in the laboratory. The smaller specimen was about 5 mm. long (fixed) and had twenty-five setigers; the gut contained about ten relatively large sand grains. The larger specimen was about 7 mm. long (fixed) and had twenty-eight setigers; there were a few small sand grains in the gut. The general appearance of these specimens resembled fairly closely that of the adult, but there were differences due to incomplete development. Thus the smaller specimen had only two pairs of branchiae, definitely recognizable as such, though the larger had fifteen, the adult number. The first and last branchiae in both specimens were very small. An interesting feature was that whilst in the adult the anterior pair of branchiae occur on the eleventh setiger the anterior pair in the smaller specimen was on the twelfth setiger and was smaller than the succeeding pair. However, there was some slight indication of the presence of branchial rudiments on the eleventh setiger suggesting that these grow at a later stage. This is in agreement with the condition of the larger specimen which bore small but distinct branchial rudiments on the eleventh setiger, whilst the second pair on the twelfth setiger were considerably smaller than on the thirteenth and immediately succeeding setigers. In the adult the first few pairs of branchiae are rather smaller than those succeeding them, but it is, nevertheless, evident that the order of appearance of the branchiae in *Ophelia* is worthy of some attention when more material is available.

DISCUSSION

Slowly the gaps in our knowledge of polychaete development are being filled, but the work that remains to be done before anything like a reasonably complete picture of polychaete embryology can be attained is very great indeed. There are still whole families for which data are either non-existent or of the most fragmentary kind. The position has changed little since my assessment of it twelve years ago (Wilson, 1936), and one has only to read Thorson's recent (1946) magnificent and painstaking compilation of old and new notes on the planktonic larvae of Danish polychaetes to be forcibly reminded of this unsatisfactory state of affairs. Thorson adds much that is new and he brilliantly summarizes many aspects, not least that of the confusion which still remains to be cleared up. 'In spite of the rather copious literature the larval Polychaetes are still poorly known' (p. 34). As he points out, the development of several common species is quite unknown.

That this should be so is not always the result of lack of effort directed to their elucidation. Several families have defied long-sustained efforts to penetrate their secrets, not least among them being the important Maldanidae and Ampharetidae, and to only a slightly lesser extent the Nephthydidae and Glyceridae. More than one worker has spent much time attempting to investigate the embryology of species belonging to these groups, with very little to show for it. From time to time, however, a species of polychaete is reared for the first time and should it happen to belong, as in the present instance, to a family whose development was previously not known, its development, even though it be of a simple straightforward type, cannot fail to be a valued addition to previous knowledge.

The development of *Ophelia* is of this simple straightforward type; its larva differs only in relatively minor details from that common to several other families of polychaetes (Syllidae, Eunicidae, Cirratulidae, Capitellidae, Arenicolidae, Terebellidae, Sabellidae). The common type is of moderate size, often rather yolky though not exceedingly so and, apart from the usual ciliated girdles (prototroch and telotroch) and ciliary tufts (apical and anal), shows no great structural specializations for swimming. Relatively few segments have been formed by the time the prototroch and telotroch are lost, that is, when metamorphosis can be said to have taken place. These segments, if setigerous, bear, as a rule, developing parapodia each with a few bristles of no great length. Slight variations of this pattern occur from family to family; sometimes a whole organ, such as the telotroch, may be reduced or absent. Some families have more yolk than others and, naturally enough, there is variation within the family, though often the development of so very few species within a family is known that on this latter point the statement rests on a little more than conjecture. The pelagic life of this typical simple form of larva is frequently, though not always, relatively short; that is, it does not extend over more than a few days (except when the post-larva is also pelagic, as in some terebellids). Food is often not taken until settlement has been effected.

In rather marked contrast to the foregoing are the larvae of some of the other polychaete families, larvae which show pronounced structural features which appear to be adaptations to a prolonged and active existence in the plankton. There may, for instance, be supernumerary rings of strong cilia (as in Spionidae and Chaetopteridae), sometimes on many segments, and there are frequently very long provisional bristles (especially well seen in Spionidae, Magelonidae, Oweniidae and Sabellariidae) which, in addition to their protective, and possibly suspensory functions, may with the aid of specialized cilia give rigidity to the body when swimming (in some, at any rate, of the Spionidae and Sabellariidae). The prototroch may be enlarged as it is in the Amphictenidae, Sabellariidae, Magelonidae and, above all, in the Oweniidae where it is sometimes looped and twisted in the manner of an echinoderm larva. A relatively spacious blastocoel is sometimes associated with an enlarged prototroch; this is especially well seen in the Oweniidae and it is a feature of the large trochosphere of *Polygordius*, and to a lesser extent of the smaller trochospheres of the Serpulidae, and perhaps one or two other families as well.

The larvae of the Aphroditidae, Phyllodocidae, Nereidae, Nephthydidae and maybe others, fall somewhere between these extremes. Thus the larvae of the polynoids have for the first part of their pelagic life a fairly well pronounced prototroch and long and numerous bristles, but their development is in many ways specialized along lines peculiar to the family. In the Nereidae there is much variation but the larvae of the family are at best feeble swimmers; some do not swim at all. Apart from their rather long bristles they resemble more nearly the simple type of larva than does the larva of the polynoids. The mode of their development fits them for early crawling rather than for prolonged swimming. The Nephthydidae and Phyllodocidae, however, contain a number of species with long planktonic lives, their larvae reaching a considerable size with numerous segments before settling. They do not possess specially long bristles and their prototrochs and telotrochs are not unduly large, though it is possible that they are specially strongly ciliated. More information is needed on these points before any definite conclusions as to the manner of their adaptation can be reached.

The development of *Ophelia* and other families with a simple larva is less specialized than the developments of the more spectacular types. Whether this is primitive or is a secondary simplification is not clear; the polychaetes are a very old group in geological time and many changes must have taken place in their ontogeny during the long period of their evolution; such points therefore are not easy to decide. It does, however, seem reasonable to suppose that long provisional bristles, enlarged prototrochs, swollen blastocoels and the other features of the more structurally complex pelagic types are adaptations which have been evolved over a very long period of time. In each family possessing one or more such structural features a somewhat standard pattern has been followed, common to the family but differing from that of other families. It is possible, in theory, to imagine that all these modifications have been produced by the exaggeration or suppression of the structures present in an ancestral simple type of larva not greatly different from that of *Ophelia*. This latter type of larva should be regarded as the typical polychaete larva and it is unfortunate that in the text-books the rather specialized *Polygordius* larva and the trochosphere of the serpulids should, apparently largely by the accident of having been among the first to be described in detail, have been taken as standard types. As long ago as 1911 Shearer pointed out the unsuitability of the serpulid larva for a text-book type and more recently Segrove (1941), working on the same family, has concurred in this. A larva such as that of *Ophelia* or of *Notomastus* has far more claim for consideration for this purpose, though there may be others, as yet undescribed, that would be even more suitable.

The projection of the posterior bristles well behind the anal extremity in the newly metamorphosed young *Ophelia* is a feature of the young of the allied *Polyophthalmus* and of mature sexual individuals of the latter also. Good figures of this are given by Stolte (1937). In adult *Ophelia* the bristles of the posterior setigers are not so pronounced, though they are moderately long and numerous, they barely pass behind the extremities of the anal papillae. In *Armandia* the last setigers bear very long capillary bristles, although it appears that the anal tube is produced beyond their backward reach. The posterior bristles of *Travisia* and *Ammotrypane* are short and rather inconspicuous. If now the grade of the bottom soil in which these various genera be considered, there becomes apparent some slight correlation with grade, for, on the whole, the finer the soil the shorter the posterior bristles. Thus *Ammotrypane* and *Travisia* inhabit fine sand and mud, *Ophelia* sands of varying grade according to the species. *Armandia* is found in coarse loose sand (Fauvel, 1925, 1927), *Polyophthalmus* among rocks and weeds (Southern, 1914; Fauvel, 1925). In the latter the bristles are specially well developed at the time of sexual maturity when the worm becomes pelagic at night. It may, therefore, be that the function of these bristles is in some way connected with the kind of bottom inhabited by the adult. What this function is can as yet scarcely be guessed, but if it be true that the length of the posterior bristles is functionally related to the grade of the soil then the relatively long bristles of the very young *Ophelia* are probably an expression of this relationship. For to the newly metamorphosed worm the sand in which it has settled is comparatively coarse, but with increasing stature becomes relatively finer. In the young, therefore, the bristles are longer in relation to the body size than they are in the adult.

Summary

Fertilizations of *Ophelia bicornis* Savigny were made and the larvae reared. This is the first time the larval development of any member of the family Opheliidae has been described.

The trochosphere is small and somewhat yolky; it has a broad prototroch, a narrow telotroch, a strong apical tuft and a long anal cilium.

Annulation is accompanied by the appearance of parapodial lobes and bristles. When the first pair of bristles of the third setiger protrude the larva is ready to metamorphose. It has two, sometimes three eyes.

The larva in its later stages can adhere strongly to solid objects, such as sand grains, by a secretion from the four anal papillae and the parapodial lobes. This is interpreted as an adaptive aid to settlement on sand banks swept by strong currents.

At metamorphosis the larval external cilia are lost and the bristles rapidly elongate, especially those of the third setiger.

Some of the larval bristles are slightly winged. So far only capillary bristles have been known in the Opheliidae.

It is pointed out that a development such as that of *Ophelia* is more typical of polychaetes as a whole than are the developments of certain species commonly used as text-book types.

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ADDENDUM

Just before going to press a paper[1] has been received from Shiro Okuda giving for the first time an account of the development of an ampharetid worm. The development is of the simple straightforward type, the larva being of moderate size, somewhat yolky, and not differing greatly from that of *Ophelia* and similar types, especially in the earlier stages.

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[1] Okuda, S., 1947. On an ampharetid worm, *Schistocomus sovjecticus* Annenkova, with some notes on its larval development. *Journ. Faculty Sci. Hokkaido Imp. Univ.*, Ser. VI, Vol. IX, pp. 321–9.

A CONTRIBUTION TO OUR KNOWLEDGE OF THE LIFE HISTORY OF *ARENICOLA MARINA* L.

By G. E. Newell, B.Sc., Ph.D.

From the Department of Zoology, Queen Mary College, University of London.

(Text-figs. 1–12)

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INTRODUCTION

A survey of the literature reveals the rather surprising fact that the breeding habits and spawning of the common British lugworm, *Arenicola marina* L., which is such a frequent and conspicuous member of the polychaete fauna of our intertidal zone, are by no means fully known.

Most of the available accounts deal with lugworms on various continental shores and there are also good descriptions of spawning and early development of the Pacific lugworm, *A. cristata.* There seem to be no recent references to the breeding of lugworms off British coastlines. Such accounts as exist are by no means in complete agreement, even on such important points as the time of the breeding season, its duration, or on the possibility of the seasonal occurrence of a pelagic spawning phase, whilst descriptions of the early development are almost completely lacking.

Thamdrup (1935), one of the more recent workers on the breeding season of European lugworms, was led, as a result of his own observations on the mud-dwelling fauna of Skalling and from results of previous authors, to put forward a 'working hypothesis', as he terms it, in order to link up the known facts. Thamdrup believed that the worms spawn in a period restricted to a few days and probably related to definite phases of the moon, in the late summer. The resulting larvae, he thought, live pelagically throughout the winter (a suggestion due to Blegvad, 1923) and then take to the bottom some time in April and June. Here they grow through the summer and winter to a size which then lies within the adult size-group range. The young worms may spawn during the second summer after they have hatched from the egg. These conclusions of Thamdrup are to a large extent based on those of Blegvad (1923) and of Pirlot (1933). Pirlot studied the lugworms of the Belgian coast, particularly at Blankenburghe. Here he noted that in September and the early part of October all the worms except the very small ones had gametes filling the coelom, but that after 15 October and throughout the winter no gametes were to be found in the body cavity. Spawning was restricted to a 2-day crisis at either the full or new moon, and in 1928 was on the 13–14 October, in 1932 on 14–15 October and in 1933 on 6–7 October. The weather had, apparently, no effect on spawning, which is probably governed by a lunar effect acting indirectly through the tides. Pirlot states that both sperms and eggs remain immature until they pass out of the body via the nephridia, and he was unable to obtain a successful artificial insemination from coelomic gametes. For this reason he remained unacquainted with the early larva. He found, however, larvae with one pair of chaetigerous segments in the sand about 14 days after the spawning crisis. In fact, with the doubtful exception of Child (1898), who merely describes fertilization and maturation (but no later stages) of the eggs of the American *A. marina*, Pirlot's failure with artificial means is typical of all other results. Naturally fertilized eggs have been recorded on two occasions. The first is that of Blegvad (1923), who was fortunate enough to find some eggs laid by worms in the aquarium at the Nyborg Biological Station. These were deposited loosely on the sand and conformed closely to the description given by Ashworth (1904). They were laid on 6 August 1923 and hatched into trochophores 4 days later. These and larvae with three chaetigerous segments were briefly described and figured. After reaching this stage of development the brood of larvae died. However, in successive Septembers Blegvad obtained larvae with five chaetigerous segments, but no stages between this and the 'post-larval' stages of Benham (1893) were seen. Post-larval stages occur in numbers in the early spring from April to June, and Blegvad believed that the pelagic larval stage must extend over the whole winter.

The second record of early larvae is that quoted by Thorson (1946), who mentions that Erik Smidt (unpublished) found newly hatched larvae crawling among the sand grains of the tidal zone at Esbjerg, but these are not described in Thorson's paper. Pelagic larvae were never found by Thorson, despite very extensive plankton hauls, and he believes that such a stage is omitted from the life cycle, the larva from the beginning being a bottom-dweller. The breeding season of lugworms in Danish waters takes place in the autumn, as is shown by the presence of coelomic gametes in August onwards for some time and by their absence in the spring. Post-larval stages as described by Benham were also not found, and it is suggested that when they occur they may be bottom stages that have been stirred up accidentally, or else they are abnormalities due to larvae metamorphosing in mid-water. The fact that young bottom-dwelling, metamorphosed worms are first met with in the summer may be explained by assuming that the young larvae settle in the autumn soon after hatching, and then stagnate until the rise in temperature of the following spring, when growth is resumed.

It will be seen from these summaries that whilst the accounts of Blegvad and Pirlot are substantially in agreement they differ in many important respects from that of Thorson and, as will be mentioned below, all three differ from those of British workers.

The possible occurrence of a pelagic stage or swarming of breeding adults has been discussed by several workers, notably by Fage & Legendre (1927), who give a useful review of what was known of the breeding habits of lugworms up to that date. It appears that the evidence for a swimming phase rests on a few but perfectly definite observations, some of which are by British observers, and on reports by fishermen. Meek & Storrow (1924), for example, noticed lugworms swimming at the surface of the sea in Northumberland for 2 days, 21 and 22 March, at the time of the full moon. The worms were enclosed in a gelatinous capsule which, it is suggested, may act as a float. All the worms were spent as if breeding had just taken place. This conclusion is, however, open to criticism, for it may well have happened that the gametes had not yet begun to develop for that season. In fact, Storrow himself (1925) noticed *Arenicola* sperms in the sand on 23–24 September 1924, which suggests an autumn breeding season. Fage & Legendre and also Pirlot (who was unable to find pelagic adults) take the view that if a pelagic phase does occur it is not directly related to the emission of the gametes.

From these various sources it would seem fair to summarize our knowledge of the breeding habits of lugworms on the shores of Europe as follows:

(i) Breeding is restricted to a period of a few days in the autumn and is probably related to spring tides. (ii) Gametes pass out through the nephridia and are fertilized in the sea. Before discharge, coelomic gametes are not fully mature. (iii) It is uncertain if the larva is a free-swimming trochophore with a lengthy pelagic life extending until the spring following hatching, or if the pelagic phase is omitted or curtailed. Recent evidence (Thorson) suggests that the latter alternative is more likely. (iv) There are almost certainly occasions on which the worms forsake their burrows and swim actively in the surface waters, but this burst of activity may, or may not, be related to spawning. The evidence here is very fragmentary. (v) All the accounts so far cited agree that the eggs are not enclosed in any sort of gelatinous capsule after they have been laid. This is an important point of difference between *A. marina* and certain other species, e.g. *A. cristata*, a Pacific lugworm common in Japan and America. The eggs of *A. cristata* and their capsules have recently been redescribed by Okada (1941), who also showed that spawning takes place at 4-day intervals from July to September during which period eggs and sperms are discharged synchronously throughout the whole habitat. Fertilization is aided by the close proximity of male and female burrows which connect one with the other so that the eggs are fertilized in them.

With regard to the breeding of lugworms in British waters it appears from the fragmentary and conflicting accounts that very little is known with certainty. Thus, Cunningham & Ramage (1888) state that in the Firth of Forth the gametes are shed in August and September. Kyle (1896), on the other hand, believed that the breeding season extends from January to September though with a cessation during April, May and early June. Gamble & Ashworth (1900) stated that the ordinary littoral forms of *A. marina* of the Lancashire coasts are not mature in the spring, but breed throughout the summer when the deeper water variety has ceased to do so. In a later publication (1904) Ashworth, who again worked at stations on the Lancashire coast and also on the Firth of Forth, states that two varieties of *A. marina* are to be found in these districts. One, smaller and abundant in the littoral zone, appears to be the form most usually met with in the British Isles and on the Continent. The other, large and having slight morphological differences from the littoral form, is restricted to the laminarian zone. Using as his criterion the presence of ripe eggs or sperms in the coelom, Ashworth concluded that the smaller, littoral variety breeds in the spring, usually from the end of February onwards for about a month or more, but he found specimens containing ripe 'ova' up to the end of April or even later. Unfortunately, Ashworth does not give any exact description of what he means by 'ripe gametes' and, as will be mentioned later, a superficial examination of the stage of maturity of the coelomic gametes gives only a rather vague indication of the time of the breeding season. The larger laminarian variety of lugworm breeds in March and onwards, but Ashworth is inclined to believe that both varieties may have a second spawning season in the late summer. This double-breeding season is certainly true for *A. ecaudata*, as mentioned by Hentschel (1930). The actual release of the gametes into the sea was not observed by Ashworth, but he believed that they pass out through the last five pairs of nephridia. He, then, like later workers, disagrees with Bohn (1903) who thought that the germ cells passed out through temporary perforations in the body wall. Full descriptions of the eggs and sperms are given in Ashworth's monograph and also an account of cleavage and early larva of *A. claparedii*, but it is stated that nothing is known of stages intermediate between the egg and the post-larval stages of Benham for *A. marina*. For British lugworms his statement would seem to be substantially correct up to the present day. Reference must, however, be made to a paper by Williamson (1916). His observations were made on the worms of the Bay of Nigg, but the species, although probably *A. marina*, was not determined in all instances. Williamson noted that ripe sperms were discharged on 2 October from worms kept in an aquarium and also believed that egg masses discharged at intervals from May to June also belonged to *Arenicola*. These egg masses were gelatinous, green in colour and contained numerous green eggs. A few days later they contained greenish embryos with two eye spots. They closely resembled egg masses found on the beaches where they were anchored by strands to the substratum or to sea weeds. Each egg mass was apparently composed of a ball of fibres loosely invested in a thin outer skin which it was believed was the cast cuticle of the female worms. In view of the wide differences between this description and those of other authors, and because other polychaetes such as *Capitella* and *Polydora* were also present in Williamson's aquarium, some doubt must attach to the view that the greenish egg masses were really spawned by *Arenicola*.

The embryology of lugworms has been fully dealt with up to the formation of the young larva by Child (1900) and by Okada (1941). Both of these authors worked on *A. cristata*. Ashworth (1904) gives a somewhat briefer description of the development of *A. claparedii*. All the descriptions are substantially in agreement, and the cell lineage seems to follow the usual polychaete plan. Descriptions of the free-living larvae of *A. cristata* are given by Lillie (1905) which agree with those of earlier workers, e.g. Child (1897).

This review serves to show that whilst a good deal is known of the breeding and embryology of foreign lugworms of various species, yet a re-examination of the life histories of British lugworms is needed to fill in gaps in our knowledge. Points which seem of particular interest are the duration and season of the year at which breeding takes place; the correlation between spawning and the tides; the method of egg-laying and fertilization; the nature and duration of larval life and a description of later stages.

This paper deals exclusively with the lugworms of the Whitstable Flats and the results may well not apply to other districts.

ACKNOWLEDGEMENTS

It is with pleasure that I tender my thanks to Mr G. P. Wells for his suggestion that I should investigate the breeding habits of the common lugworm. Not only has he given me much help and encouragement but has also very kindly read through the manuscript. Mr D. P. Wilson was kind enough to give me considerable help with the literature. The work has proved a good deal more arduous than I expected and the records I have kept could not have been so complete were it not for the very considerable help I have received from my small children who throughout the severe winter of 1946–47 helped me collect my specimens. Mr Cullen of Queen Mary College took the photographs of the developing eggs and to him I am extremely grateful.

THE BREEDING SEASON

As already mentioned, there is considerable disagreement in the literature as to the time and duration of the breeding season of *A. marina*, some sources stating that it occurs in the spring, others in the autumn. All accounts dealing with British lugworms, with the possible exception of Meek & Storrow (1924), indicate a protracted period in contrast to a concerted spawning, or crisis, as described by some continental workers for the same species. Over a period of many years it has been noticed that the lugworms of the Whitstable Flats have their body cavities full of germ cells throughout the late summer and early autumn and that by the end of October all the worms are 'spent'. This clearly points to a breeding season in early autumn. A further point noticed in a purely qualitative way is that the worms are very much scarcer in the winter than in the summer and the impression was gained that the drop in numbers occurred rather suddenly at about the middle or end of October. If this is, in fact, true then it indicates a mortality among the spawning adults or else a migration related to spawning. It seemed that a record of the density of the worm population over a whole year, in conjunction with observations on the state of sexual maturity, would throw a good deal of light on both these points. Accordingly, with a few exceptions due to adverse weather or tides, worms were dug at weekly intervals, or even more frequently, throughout the period November 1946 to November 1947. Each sample was collected from the same general area of the Flats about 50 yards seaward of the pebble and *Fucus* zone (Fig. 1). Each sample was usually in excess of forty worms and sampling was carried out in each instance by digging up areas measuring 6 ft. × 1 ft. 6 in., giving areas of 1 sq. yd., so that the density of the worm

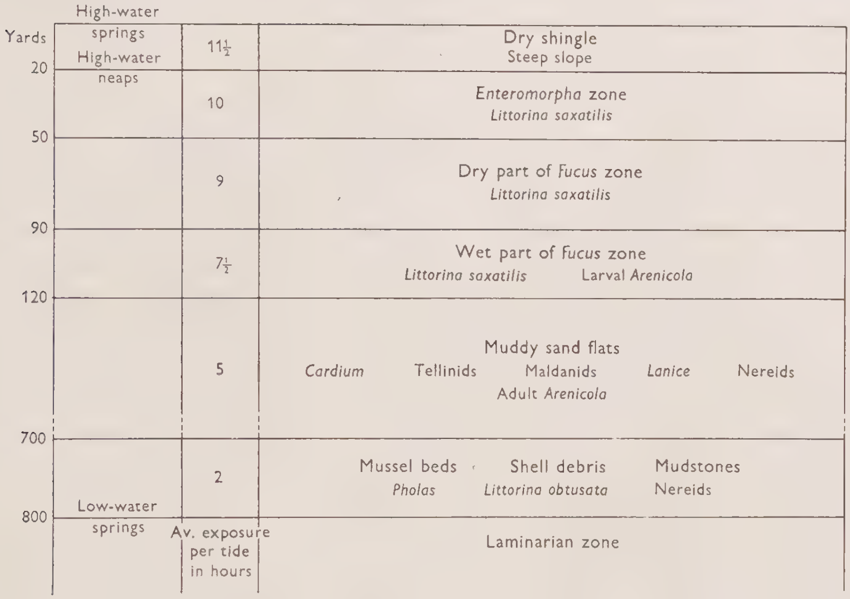

High-water springs
High-water neaps
Yards
20
50
90
120
700
800
Low-water springs
Av. exposure per tide in hours
11½
10
9
7½
5
2
Dry shingle
Steep slope
Enteromorpha zone
Littorina saxatilis
Dry part of *Fucus* zone
Littorina saxatilis
Wet part of *Fucus* zone
Littorina saxatilis
Larval *Arenicola*
Muddy sand flats
Cardium
Tellinids
Maldanids
Lanice
Nereids
Adult *Arenicola*
Mussel beds
Pholas
Shell debris
Littorina obtusata
Mudstones
Nereids
Laminarian zone

Fig. 1. Diagram to show the approximate zonation and some of the commoner animals of the intertidal zones.

TABLE I. AVERAGE NUMBER OF WORMS PER SQUARE YARD, NOVEMBER 1946 TO NOVEMBER 1947

	Month	Average number per sq. yd.	Coelomic gametes	
1946:	November	8·4	—	
	December	10·0	No gametes in coelom	
1947:	January	10·1		
	February	10·0		
	March	12·0		
	April	14·2		
	May	19·0		
	June	17·0	Gametes maturing in coelom	10 % adults 'milky'
	July	16·5		80 % adults 'milky'
	August	16·9		95–98 % adults 'milky'
	September	18·5		98 % adults 'milky'
	October	19·0		98 % adults 'milky'
	November	—	No gametes in coelom	
	December	—		

TABLE II. AVERAGE NUMBER OF WORMS PER SQUARE YARD, PERCENTAGE WORMS 'MILKY', ETC. OCTOBER TO NOVEMBER 1947

Date	Av. no. per sq.yd.	% worms 'milky'	Phase of moon		Remarks
1 Oct.	20	99	—		—
2	19	99	—		—
3	20	98	—		—
4	19	97	—		—
5	18	99	—		—
6	19	98	—		—
7	20	98	L.Q.		—
8	19	—	—		—
9	18	—	—		—
10	18	—	—		—
11	18	—	—		—
12	17	—	—		—
13	17	98	—		—
14	18	—	N.M.		—
15	18	—	—		—
16	18	98	—	Spawning period	Puddles of sperm observed at low tide. Spring tides
17	17	98	—		—
18	19	—	—		—
19	18	—	—		—
20	20	—	—		—
21	20	—	—		—
22	19	—	F.Q.		Max. number of puddles of sperms
23	18	—	—		—
24	20	—	—		Neap tides
25	20	60	—		—
26	19	—	—		—
27	—	—	—		
28	—	—	—		Approx. 40 % mortality of spawning adults. No spawning seen. Spring tides
29	18	8	F.M.		
30	15	5	—		
31	—	0	—		
1 Nov.	12	0	—		
2	—	0	—		
8	8	0	—		

population could easily be expressed in numbers per square yard. This rather tedious method of sampling was found to be essential, since counting the number of casts per square yard is a most unreliable index of the number of worms, varying as it does with, among other conditions, the state of the tide. For most of the year there was little variation in the numbers of worms per square yard from week to week, and for simplicity the results have been consolidated and given as monthly results. For September and October, however, more frequent results are given. The results are given, together with remarks on the state of sexual maturity and phases of the moon, in Tables I and II and Figs. 2 and 3.

Discussion of Results

It will be noticed from Table I and Fig. 2 that the average number of worms per square yard rises throughout November and December, remains at about 10 per square yard during January and February and then reaches the high figure of 19 per square yard in May. From this point onwards, until the end of October, it is fairly constant at between 17 and 21 per square yard. There is a very marked sudden decrease in numbers on or about 31 October.

The soil from which the worms were dug is a favourite area for bait diggers and minor fluctuations in the numbers of the worms may probably be attributed to their activities. The digging of lugworms for bait, cannot, however, account for any substantial decreases in the worm population, for more bait is dug throughout August and early September than at any other period of the year and yet the density of worms remains high. Furthermore, there is practically no bait dug in the middle of the winter when the worm population is at its lowest (November to February), and the numbers continue to increase from February to May during the later part of which period bait diggers resume their activities. It can be assumed, therefore, that the density of the worm population is virtually unaltered by the interference of man, and some other explanation must be sought for any striking variation in the number of worms per square yard of the soil.

An observation made in October 1946 gave a clue to the cause of the sparcity of worms in the late autumn and winter of that year, for on 26 and 27 October, on which there were neap tides, large numbers of spent worms were found cast up dead on the shore. Previous to these dates worms were plentiful, but afterwards were scarce. Unfortunately, quantitative observations had not then begun, so that no figures can be given for this period. Before the end of September 1946 the overwhelming majority of the worms were of a milky appearance owing to germ cells packing their body cavities, but of the worms remaining in the Flats after this date few only were milky, although about 75 % retained a few germ cells until the end of October. By the beginning of November all were completely spent.

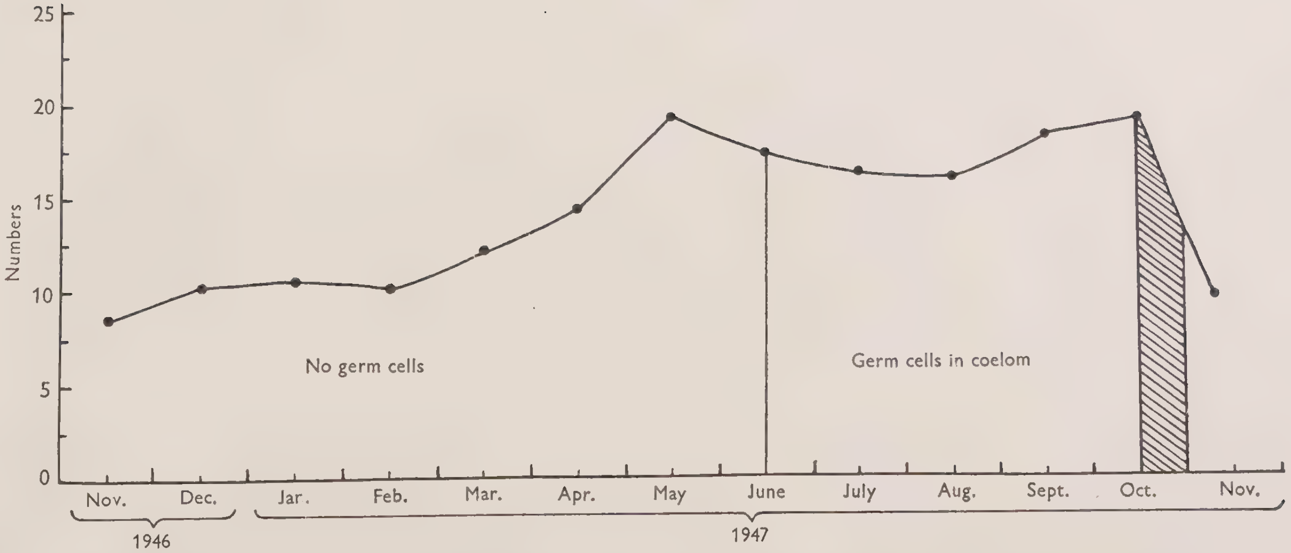


Fig. 2. Monthly variation in numbers of worms per square yard of soil dug. Shaded portion indicates spawning period.

The upshot of these preliminary observations is that the breeding season of the lugworms of the Whitstable Flats is during a period in the autumn which agrees with statements of Blegvad (1923), Pirlot (1933), Thamdrup (1935) and Thorson (1946), whereas Kyle (1896), Ashworth (1904) and others believed the breeding season to extend through the spring and early summer. The drop in numbers noted would seem in some way to be related to spawning.

As has been seen, the general conclusions are borne out and amplified by the records kept during the period November 1946 to November 1947. From Table I it will be seen that germ cells in any quantity first make their appearance in the coelom in June when about 10 % of the worms appear milky. From June to the middle of October the germ cells multiply and mature, and from August onwards, until the end of October, 98 % or more of the worms are 'milky'. After 31 October all the worms are spent, although it is true that in about 5 % of the worms a few ripe eggs and sperms could be detected, but then only in specimens dissected under a binocular microscope. They are so few in number that they can play no significant part in the main spawning process. Tables I and II clearly indicate that spawning ends on, or near to, 31 October, but they give no exact information as to when it begins. Fortunately, other evidence is available. On 16 October and onwards, until 31 October, small puddles of white fluid were noticed on the wet sand of the Flats. These proved to consist of lugworm seminal fluid containing active sperms. None was seen before dead low tide and it was later observed that the discharge of seminal fluid takes place all over the area within about half an hour. On several occasions sperms were seen being pumped out of the exit from the tail shafts of the worm burrows. Observations over the spawning period showed that spawning, as indicated by the number of sperm puddles, began slowly, reached a maximum intensity on 25 and 26 October and then decreased to finish on 31 October. Examination of the worms at intervals also suggests very strongly that each worm can spawn several times in the fortnight,

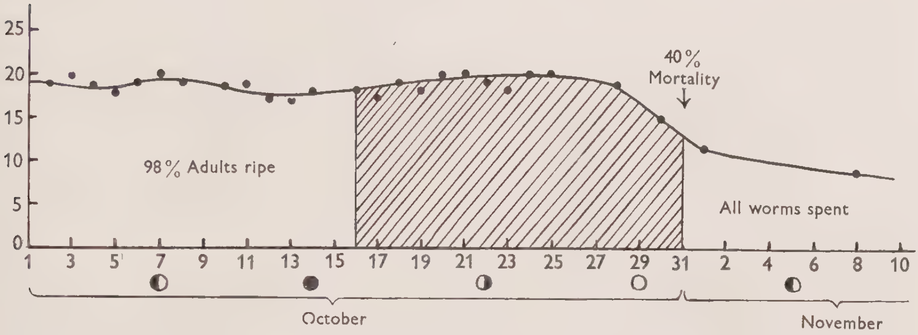


Fig. 3. Average numbers of worms per square yard of soil dug in October and November 1947
Shaded portion indicates spawning period.

for there is an obvious decrease in the number of germ cells in the body cavity, although this is difficult to assess quantitatively. Not all the worms, however, become exhausted of germ cells at the same time, as is shown in Table II. Here also is indicated the relation of spawning to the phases of the moon and to spring and neap tides. It will be seen that spawning begins and ends on a spring tide, but is most intense at the intervening neap tides. The dates, but not the tidal relations, are similar to those noted by Pirlot (1933) for the lugworms of the Belgian coast. How strictly spawning is related each year to a particular moon is not known, but there is some evidence that spawning in 1946 was about a fortnight earlier than in 1947 and would then have been related to the period between the spring tides following the new moon of 25 September and those following the full moon of 10 October.

During the period 16–31 October close watch was kept for eggs on the surface of the sand, but none were seen. It was assumed that this was because the eggs are so similar in colour to the sand that they are virtually invisible. That the eggs like the sperms are, indeed, passed out of the burrows and deposited on the surface of the sand was proved by finding eggs on several days in samples of water in which sand from the surface of the flats had been stirred up and sieved through a plankton net. Also, on 29 October some worms spawned in the aquarium in London. When the females were spawning they frequently protruded their heads for a short time above the surface of the sand. The eggs also were passed out through the head shafts of the burrows near to which they remained until disturbed, so that it seems clear that the burrows conformed to the U-shaped variety described by Wells (1945). These females spawned on several successive days, thus confirming the conclusion reached from a study of the worms in their natural surroundings. The eggs laid in the aquarium proved to be fertilized and a brief account of their development is given below (pp. 568–70).

To sum up, it may be stated that lugworms of Whitstable, and almost certainly of neighbouring districts, spawn during 2 weeks in early autumn in the period between two spring tides. The spawning period, although sharply defined, is not a 2-day crisis as described by Pirlot, nor is it an extended one as was believed by Ashworth and others. There is only one spawning period in each year and the actual dates vary with phases of the moon. A decrease in the lugworm population takes place rather suddenly towards the end of, and immediately after, the spawning period. It is almost certainly due to death of about 40 % of the adults (probably those which have spawned) and accounts for the smaller numbers of worms present during the winter (see also pp. 575–7). Some of these dead worms were found in their burrows on 8 November 1947, but in this year none was seen floating in the sea.

MATURATION AND STRUCTURE OF THE GERM CELLS

As is well known from the descriptions of Ashworth and others, the gonads are situated immediately behind the coelomic funnel of each nephridium. They remain minute in size, and for some considerable time before the breeding season immature oocytes and spermatogonia are shed from the gonads into the coelom, where they accumulate and give to the worms a milky appearance. The germ cells grow and mature in the coelom, but the oocytes, although gaining their full size, remain as primary oocytes until after they are fertilized.

It can be stated quite definitely that the lugworms of the Whitstable district for the greater part of the year, namely from the end of October until June, have no appreciable quantities of germ cells maturing in the body cavity. In 1947 the first time that germ cells were noticed was in June, when about 10 % of the adult worms had small numbers of oocytes or spermatogonia floating in the coelomic fluid. This conflicts with the findings of Ashworth (1904) for the lugworms of the Lancashire coast, for he states that 'the body cavity of large worms is filled with them almost to bursting by about the end of February' and that 'specimens containing ripe ova may be occasionally met with up to the end of April'.

Ashworth's description of the maturation of the germ cells agrees in essentials with what has been found for the Whitstable lugworms, and a redescription in detail seems, therefore, not to be called for. However, the results of the present investigation, together with any divergences from previous accounts, are summarized below. In mid-June maturing coelomic germ cells could be detected with the aid of a hand-lens in about 10 % of the specimens dissected and it is probable that a higher percentage of worms had germ cells already liberated into the coelom, but that these escaped detection by the rough and ready methods which were employed on the shore. Previous to this date, by the same standards, no worms had any coelomic germ cells. More detailed examination revealed that the oocytes were practically spherical cells, only slightly flattened in the plane at right angles to the main egg axis. They had a largest diameter which varied from 0·07 to 0·08 mm., whilst the nucleus had a diameter of about two-thirds that of the cell. The developing male germ cells were in the form of thick disk-like masses of spermatogonia of varying size.

By the middle of July, 80 % of the adult worms were full of germ cells, even down to the end of the tail, but these seemed not to have advanced appreciably towards maturity. At the end of August 98 % of the worms were 'milky'. Throughout the month of September 90 % or more worms were 'milky' and coelomic germ cells were examined at fairly frequent intervals. By 8 September all the oocytes were much alike in size, being discoidal cells, usually with a circular outline but sometimes slightly oval, and having a diameter of 0·17 mm. and a depth of 0·08 mm. The main egg axis was at right angles to the plane of flattening. The cytoplasm is orange in colour and very opaque, whilst the nucleus appears in the living oocytes as a clear vesicle with a diameter of 0·06 mm. The egg cytoplasm is full of yolk granules and has a great affinity for most stains, including haematoxylin, but permanent preparations are extremely difficult to make successfully. The vast majority of the male germ cells were spermatids, still united into flattened masses by residual cytoplasm. A few (about 10 %), however, had metamorphosed into spermatozoa, although the tails showed no signs of motility. The heads of the spermatozoa remained attached to the central mass of cytoplasm termed by Ashworth the blastophore (Fig 4, C and D).

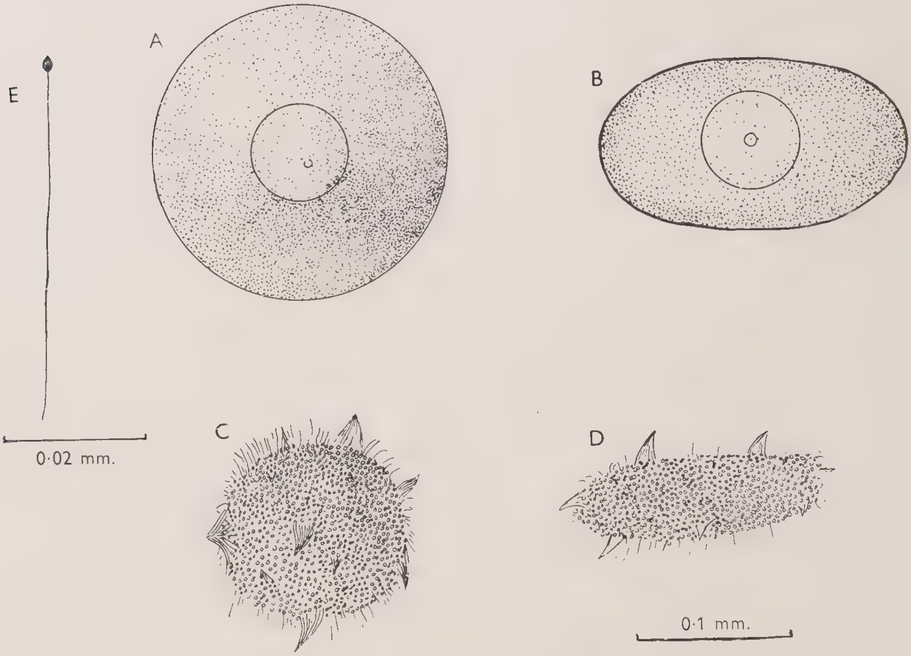


Fig. 4. A, fully grown coelomic oocyte. B, the same in side view. C, disk of mature sperms. D, the same in side view. E, mature spermatozoon. A, B, C and D approx. × 210. E approx. × 1000.

By 28 September the oocytes had grown to have a diameter of 0·175 mm. and a depth of 0·095 mm. (Fig. 4, A and B). Little change was noticed in the male germ cells. The next detailed examination was made on 8 October, when the oocytes had attained a diameter of 0·18 mm., but apart from this had the same appearance. In the male worms about half the sperm masses consisted of spermatozoa. On 15 October most of the sperm cells had acquired tails and some of them had limited powers of movement. In many of the sperm masses the sperm tails were united by their tips and their slow undulations had rather the appearance of a flagellar 'flame'. The significance of this is obscure. The oocytes by this time had attained a diameter of 0·19 mm. It is in this stage that both male and female germ cells are discharged.

Comparison with Ashworth's diagrams and figures of the dimensions of the oocytes reveals that the oocytes of the Whitstable worms are slightly larger (0·19 mm. as compared with 0·15 mm.). They also differ in shape being only very slightly biconvex or even biconcave and not strongly biconvex disks. Each oocyte is surrounded by a thin but tough vitelline membrane and after being left for some time in sea water this membrane acquires a certain stickiness and the eggs adhere quite firmly to the bottom of a glass vessel. They are appreciably heavier than water and this, combined with their adhesiveness, would tend to make them remain in the sand instead of being carried away in the plankton.

The spermatozoa of *Arenicola marina* have been described and figured by Ashworth, and those of *A. cristata* by Okada who also gives a detailed account of gametogenesis. Whilst Ashworth reported a distinct middle piece, Okada finds that this is incorporated in the head. The accounts of the two workers differ also in the shape of the head, particularly of the acrosome. The dimensions given in each account are of the same order of size if it is assumed that Ashworth's figure of 0·04 mm. for the length of the head should read 0·004 mm.

Spermatozoa collected in October 1947 had a total length of 0·055 mm., whilst the head measured 0·004 mm. in length. The general form is shown in Fig. 4 E. Very little detail could be made out and no distinct middle piece could be detected, the tail appearing to arise directly from the head.

Discharge of the Germ Cells

As far as is known there have been no direct observations of the discharge of the germ cells from the body in *A. marina*, but practically all workers are agreed that the gametes pass out through the nephridia. This is certainly true for *A. cristata* (Okada, 1941). Ashworth noticed germ cells distending the bladders of the nephridia, but dissections of many worms during the breeding period of 1947 failed to give confirmation of this observation. Nevertheless, the germ cells are discharged without any apparent rupture of the body wall, so that it is reasonable to infer that the nephridia do function as gonoducts, but that the gametes pass out through them very rapidly.

Sex Ratio

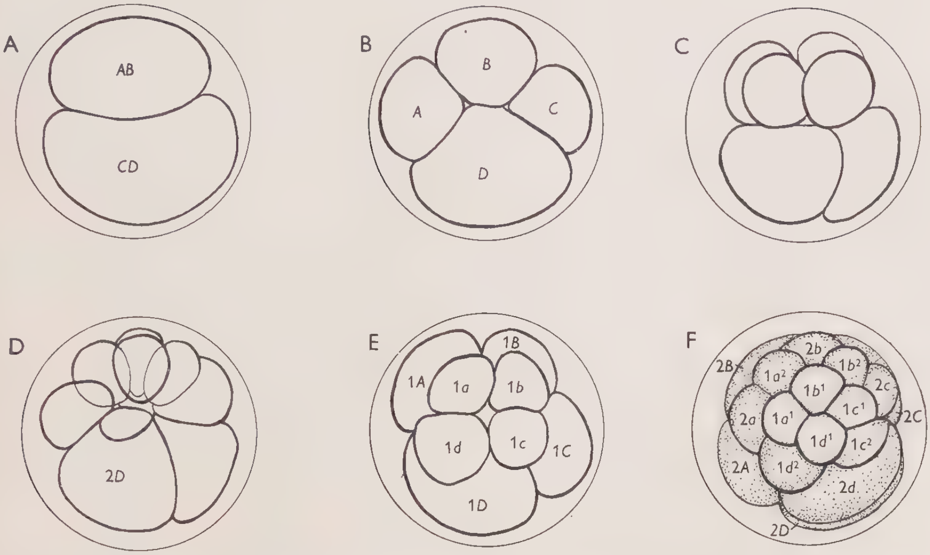
Difficulty in finding ripe males amongst an abundance of ripe female worms suggested that there might be a differential sex ratio. Counts on 300 worms showed that this was, indeed, true, the ratio being 3·7 females to 1 male in August and 3·8 females to 1 male in September. Okada, on the other hand, found a 1:1 sex ratio for *A. cristata*, so that in this as in other respects the Japanese differs from the British lugworm.

ARTIFICIAL INSEMINATION

It was found that mature spermatozoa, although still attached to the central mass of cytoplasm whilst they are in the body cavity and for a short time after they are discharged, rapidly gain their independence after a short time in sea water. Masses of coelomic sperm soon acquired motility and swam actively when transferred artificially to sea water, particularly if it was slightly hypotonic. There seems no obvious reason why sperm taken from the body cavity of ripe males and activated in sea water should not be capable of fertilizing what were apparently fully ripe oocytes from the coelom of ripe females. Yet all previous attempts at artificial insemination have come to nothing. In fact, Pirlot states definitely that the coelomic gametes are not viable until they have passed through the nephridia. Experiments carried out in October 1947 suggest that his statement is only partially true, for coelomic oocytes were induced to mature by artificial insemination with coelomic sperms to produce a fertilization membrane and undergo two cleavages. On another occasion sperm which had been shed in the natural way was collected from the sand and added to oocytes taken from a ripe female. The spermatozoa were fully active and yet the oocytes did not develop beyond the 4-cell stage. This tends to show that the inadequacy for development is a property of the oocytes rather than of the spermatozoa. Unfortunately, the converse experiment was not carried out because of failure to find unfertilized eggs naturally discharged on to the sand.

EARLY DEVELOPMENT OF THE EGG

The eggs are fertilized on or in the superficial layers of the sand, presumably shortly after the discharge of the sperm near the time of dead low water. They are then covered merely by the shallow layer of water left by the retreating tide between the sand ripples. This timing certainly must increase the chances of fertilization, preventing as it does undue dilution of the seminal fluid. Tests carried out in the laboratory, however, show that spermatozoa remain motile for at least 18 hr. Observations on coelomic oocytes, to which had been added naturally discharged sperms, revealed that almost immediately the oocytes become surrounded by many hundreds of spermatozoa which cling to the vitelline membrane and by their activity often cause the egg to rotate. Sperm entry was not observed, but after $1\frac{1}{2}$–2 hr. most eggs had developed a 'fertilization membrane', and soon afterwards the first polar body was cut off. After 2–$2\frac{1}{2}$ hr. two polar bodies could be seen, both lying inside the egg membrane. Comparison of the diameters of unfertilized and fertilized eggs shows that the lifting clear of the fertilization membrane is due, in part at any rate, to shrinkage of the contents of the egg. With the formation of the fertilization membrane the egg loses its flattened shape and becomes practically spherical. Crossing the perivitelline space are what appear to be delicate threads of cytoplasm.


A
AB
CD
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B
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D
C
D
2D
E
1B
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1a
1b
1d
1c
1C
1D
F
2b
2B
1a²
1b²
2c
1b¹
2a
1a¹
1c¹
2C
1d¹
1c²
2A
1d²
2d
2D

Fig. 5. Camera lucida drawings of cleavage stages. A, 2-cell stage. B, 4-cell stage from animal pole. C, 8-cell stage from the side. D, 2nd quartet of micromeres being formed. E, 8-cell stage from the animal pole. F, 16-cell stage from the animal pole.

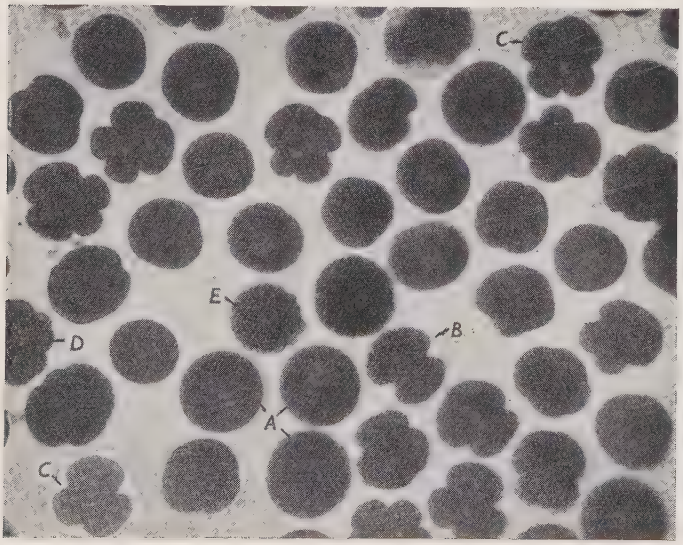

Fig. 6. Untouched photomicrograph of living cleavage stages. A, fertilized egg. B, 2-cell stage. C, 4-cell stage from the animal pole. D, 16-cell stage. E, blastula.

The first cleavage begins about 3 hr. after fertilization, is completed fairly rapidly, and results in the formation of two very unequal-sized blastomeres, the larger one, *CD*, lying posterior to the smaller one, *AB* (Fig. 5). The second cleavage, also in a vertical plane but at right angles to the first, divides blastomere *AB* into two cells, *A* and *B*, and *CD* into *C* and *D*. Of these *A*, *B* and *C* are all approximately equal in size, but *D* is much larger. The third cleavage is a horizontal one and, as in other polychaetes, results in the formation of the first quartet of micromeres, 1*a*–1*d*. Each of these is cut off obliquely so that it lies above but to the right of its corresponding megamere. Cleavage is, then, of the familiar spiral type and, as far as could be seen, it follows almost identical lines to that described fully for *A. cristata* by Child (1900) and Okada (1941) and by Ashworth (1904) for *A. claparedii*. No attempt was therefore made to follow the details of cleavage and gastrulation. Neither would this have been at all easy, for the developing eggs are singularly opaque and difficult to make into permanent preparations. The photomicrographs and outline drawings of living cleavage stages give some idea of early development (Figs. 5 and 6).

After 4 days a few larvae (Fig. 7) hatched, but the rest of the embryos died, since it was difficult to maintain satisfactory conditions in the small aquarium which alone was available. The larvae, like the eggs, are very opaque and creamy pink in colour. They are about 0·24 mm. long, and shaped rather like a radish. There is a well-defined prototroch encircling the thickest part of the body at about one-quarter of the way from the anterior end. A telotroch encircles the hinder end of the body and there is a prominent apical tuft of long cilia. Some distance behind the apical tuft, but on the dorsal side, is a pair of dark brown eye spots, whilst along the ventral surface, between the prototroch and the telotroch, is a band of shorter cilia. Neither mouth nor anus appears to be formed, but owing to the opacity of the larvae little could be seen of the internal structure, either in living larvae or in stained mounts. This is unfortunate, because only brief descriptions of early *A. marina* larvae are available. In fact, the only account that has been found is that of Blegvad (1923), who reared a few up to the time when three chaetigerous segments had differentiated. He also states that he found in September larvae with five chaetigerous segments, but gives no description of these nor does he mention where or how they were collected. Pirlot also found larvae with one chaetigerous segment in the sand, but neither describes nor figures them. Thorson (1946) mentions that E. Smidt has discovered early larvae, but again no description of them is given. He has, however, reasons for believing that from the first the larvae develop on the sand and remain there to develop further without ever becoming pelagic. Some confirmation of this view was found in the habits of the newly hatched larvae found in October 1947 for, unlike those of *A. cristata* (*vide* Lillie, 1905) or of *A. claparedii* (*vide* Ashworth, 1904), they often remained attached by their posterior end to the bottom of the dish and

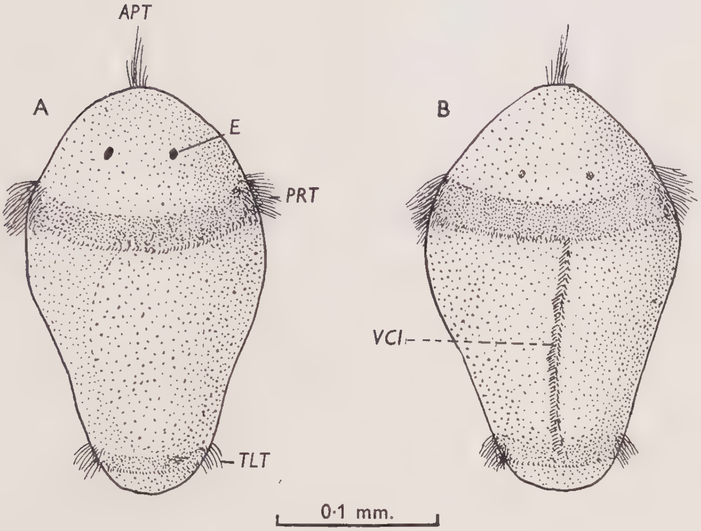
APT
A
E
PRT
B
VCI
TLT
0·1 mm.

Fig. 7. Camera lucida drawings of newly hatched larvae. A, dorsal view. B, ventral view. *APT*, apical tuft; *E*, eye; *PRT*, prototroch; *TLT*, telotroch; *VCI*, ventral ciliated band.

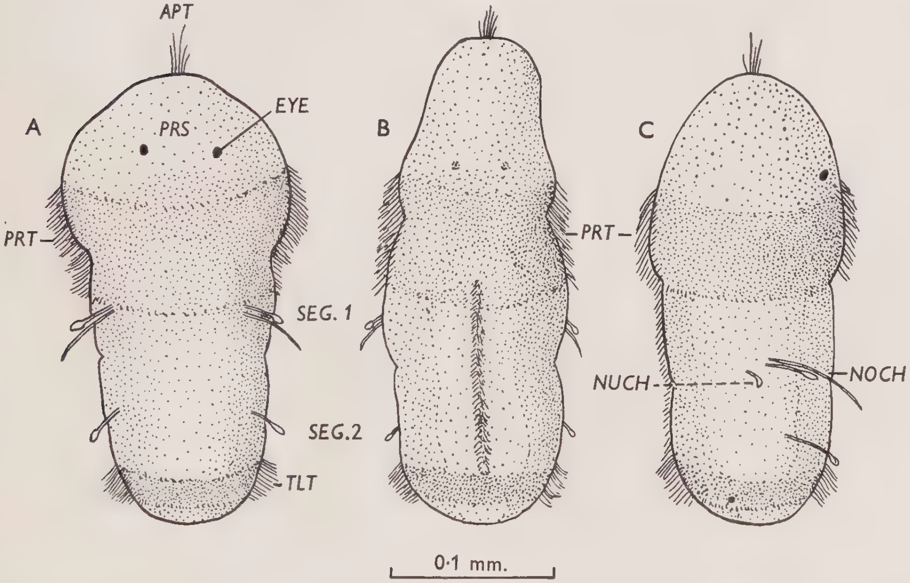
APT
A
PRS
EYE
B
C
PRT
PRT
SEG. 1
NUCH
NOCH
SEG.2
TLT
0·1 mm.

Fig. 8. Camera lucida drawings of living larvae with two chaetigerous segments taken from the *Fucus* zone. A, dorsal view. B, ventral view—prostomium extended. C, side view. *APT*, apical tuft; *EYE*, eye; *NOCH*, notopodial chaetae; *NUCH*, neuropodial chaetae; *PRS*, prostomium; *PRT*, prototroch; *SEG*, segment; *TLT*, telotroch.

returned to this position almost immediately if they were forcibly detached. They can, however, swim quite rapidly for short distances. Also, repeated hauls with a plankton net immediately after and during the breeding season failed to capture any larvae, a result which agrees precisely with that of Thorson. The newly hatched larvae can, however, undergo considerable and rapid changes in shape and can crawl about on the substratum, seemingly well adapted from the first to a bottom-dwelling existence. That Thorson was undoubtedly correct was proved on 8 November 1947, when large numbers of larvae with two chaetigerous segments were obtained by straining through a plankton net water which had been stirred up with sand. They were taken from the shallow pools which are common in the seaward half of the pebble and *Fucus* zone and which have fine sand and mud mixed up with the shingle. All the larvae (Figs. 8 and 9) were at much the same stage of development and must have been hatched about 14 days previously. Careful search failed to detect any of the larvae in the sand of the Flats which lie beyond the pebble zone and in which the spawning adult worms live, and it must be assumed that the fertilized eggs were carried towards the shore by the advancing tides and were deposited (being heavier than water) in the pebble zone as the pace of the tide slackened towards high water. Once in among the stones the larvae or eggs would be protected from currents and would tend to remain in the crevices. It is worthy of note that debris of all kinds is deposited in the same area but particularly at the high-tide mark. The coincidence of the maximum spawning intensity with neap tides is an interesting adaptation favouring the deposition of most of the eggs in a favourable zone, since the high-tide mark at these tides rarely passes the *Enteromorpha* zone whereas, during spring tides, the high-water mark is well up on the dry pebbles and sand of the beach proper where eggs and larvae would undoubtedly perish. The fact that the larvae can swim actively for short periods will, of course, increase the chances of the larvae finding suitable surroundings in which to settle, but what conditions constitute a favourable environment can only be guessed at. Shelter between the stones, fine silt and a plentiful supply of fine vegetable debris may perhaps be of importance.

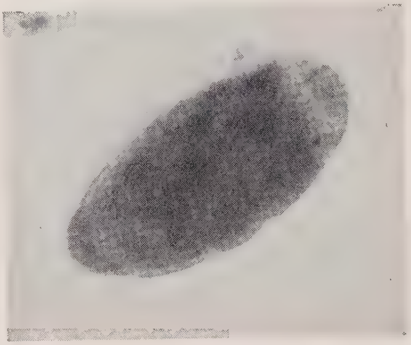

Fig. 9. Untouched photomicrograph of living larva with two chaetigerous segments.

The larvae with two chaetigerous segments are just visible to the naked eye as white specks about 0·25 mm. in length, and at first glance much resemble a small planarian. When at rest the body is bluntly conical, the broader end being anterior. Here is borne the apical tuft, whilst a little distance behind on the dorsal side is a pair of dark brown eyes. Two rather indistinct grooves mark off the two segments. In the youngest of these larvae the anterior chaetigerous segment bears two notopodial chaetae, one of which is spoon-shaped and the other spear-shaped, but in some larvae this segment had also a single hooked neuropodial chaeta. The second chaetigerous segment bears a single chaeta only, which is spoon-shaped. Both prototroch, telotroch and ventral ciliated band are still present, but much wider, and it is by means of these that the larvae swim rapidly when detached from the bottom. Usually they crawl among the sand grains and detritus among which they live. They are extremely muscular little organisms, the prostomial region particularly being capable of a high degree of contraction and expansion. Reference to the descriptions of the larvae of *Arenicola cristata* given by Lillie (1905) and Okada (1941) and of *A. claparedii* by Ashworth (1904) will show that the larvae of *A. marina* are very similar to those of *A. cristata*, but hatch at a slightly earlier stage, having at first no chaetae. They are in this respect more like those of *A. claparedii*, but develop more slowly.

Apparently nothing is known of the structure and mode of life of larvae intermediate between those with three chaetigerous segments and the post-larval stages of Benham (1893) which are occasionally taken in plankton hauls in the spring.

During this investigation evidence has been found for the view that the larvae remain throughout the winter in the top centimetre or two of the sand in or bordering the seaward edge of the *Fucus* zone. By the following spring they have metamorphosed and grown into small worms resembling the adults in all essential features. Certain it is that small worms about 1·5 cm. long are found for the first time each year in enormous numbers in this region and not elsewhere on the Flats.

There is every reason to be hopeful that some of the so-far missing intermediate larval stages will be found during the coming winter.

Size Groups and Growth Rates

The very extensive samples taken from the lugworm population at fairly regular intervals over the whole year November 1946 to November 1947 provided material which was used to gain some idea of the growth rates and of the age and size groups. For these purposes the length of the body, excluding the tail, of freshly dug worms was measured. This gave a more reliable index of size than does total length of the body, since the tail (posterior achaetous region of the body) varies greatly in its proportion to the rest of the body, being frequently shortened by damage and often almost absent. Lengths were measured only to the nearest 0·5 cm., except on specimens of a year or less in age. The lengths refer to specimens in a moderate degree of contraction, a condition that they usually adopt a few seconds after being handled. The

TABLE III. AVERAGE LENGTH OF THE BODY (EXCLUDING THE TAIL) IN CM.

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
Young worms	—	—	—	—	—	0·8	1·5	2·0	2·4	3·75	4·3	4·0
Total worm population	6·4	5·5	5·3	4·8	5·9	6·1	8·2	8·1	9·2	9·1	9·8	8·7

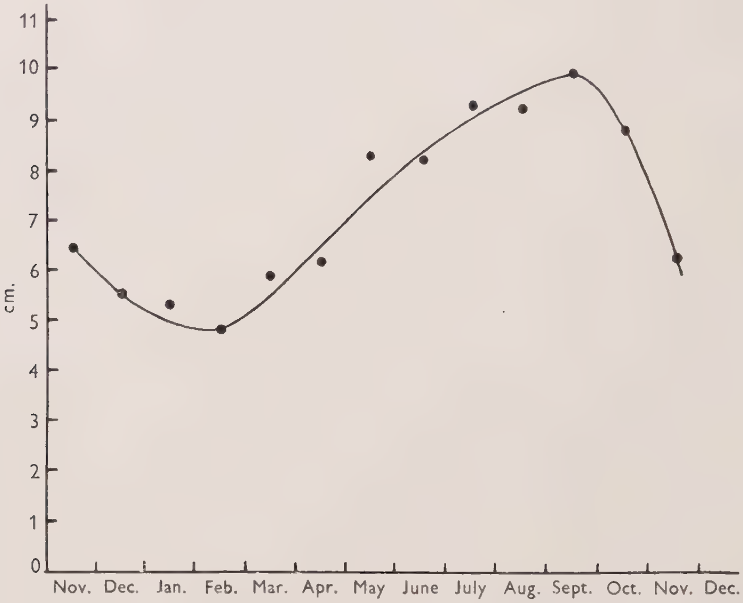

Fig. 10. Average length of body (excluding tail region) of adult worms.

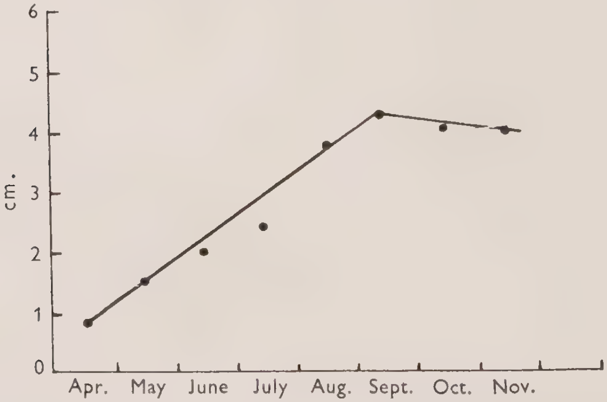

Fig. 11. Growth curve of young worms as shown by average monthly length of body (excluding tail).

results, although only approximate, gain in value from the very large number of worms which were measured.

The monthly figures for the average length of the body, excluding the tail, of all the worms collected are given in Table III and are expressed graphically in Fig. 10. Table III, also, and Fig. 11 show separately the average monthly lengths, excluding the tail, of young worms from eggs spawned in the autumn of 1946. These worms are easily separable from all others by their small size, pinkish colour and, usually, by being found nearer the shingle beach.

TABLE IV. CENTIMETRE SIZE GROUPS IN WORM POPULATION EXPRESSED AS OUT OF 200 WORMS

Size group (cm.)	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
2–3	—	—	3	3	1	1	—	—	—	—	—	—
3–4	4	20	21	26	11	7	1	—	—	1	1	2
4–5	16	25	40	43	31	15	1	7	1	2	8	2
5–6	38	85	61	73	62	33	12	21	3	8	2	7
6–7	63	55	47	36	47	59	27	23	12	14	11	21
7–8	58	15	29	16	31	31	48	48	37	24	20	43
8–9	20	—	5	3	11	23	39	46	38	35	13	41
9–10	—	—	3	—	5	15	34	19	38	33	22	21
10–11	—	—	—	—	1	7	18	18	16	30	45	24
11–12	—	—	—	—	—	4	12	7	20	23	28	21
12–13	—	—	—	—	—	3	5	5	19	12	20	13
13–14	—	—	—	—	—	—	1	3	7	14	11	5
14–15	—	—	—	—	—	—	1	—	7	3	8	3
15–16	—	—	—	—	—	—	—	2	1	1	—	—

The same figures were used to construct histograms (Table IV and Fig. 12) which show for each month the numbers of worms (to the nearest whole number) in a series of size groups which differ from one another by 1 cm. in length of the body, excluding the tail. Since the actual size of the samples was rather variable, the figures have been expressed as numbers out of 200. It should be mentioned that these figures all refer to worms obtained from the same general area of the Flats about 50 yd. seaward of the pebble and *Fucus* zone. They do not, until April, include any of the 1946 brood of worms and even after this time young worms are exceedingly rare in this area until November, and so are lacking from some monthly samples.

Discussion of Results

From Table III and Fig. 10 it will be seen that the average length of the worms decreases from about 6·4 cm. in November to 4·8 cm. in February, and then rises steadily to reach a maximum in September when the length index is 9·8 cm. This is followed by a fairly sharp decrease in October and November 1947 until the average length index is only 6·2 cm. Young worms, from eggs spawned in the previous autumn, grow from 0·8 cm. in April to 4·3 cm. in September and then decrease to a length index of about 4·0 cm., which probably remains fairly constant throughout the winter. By the

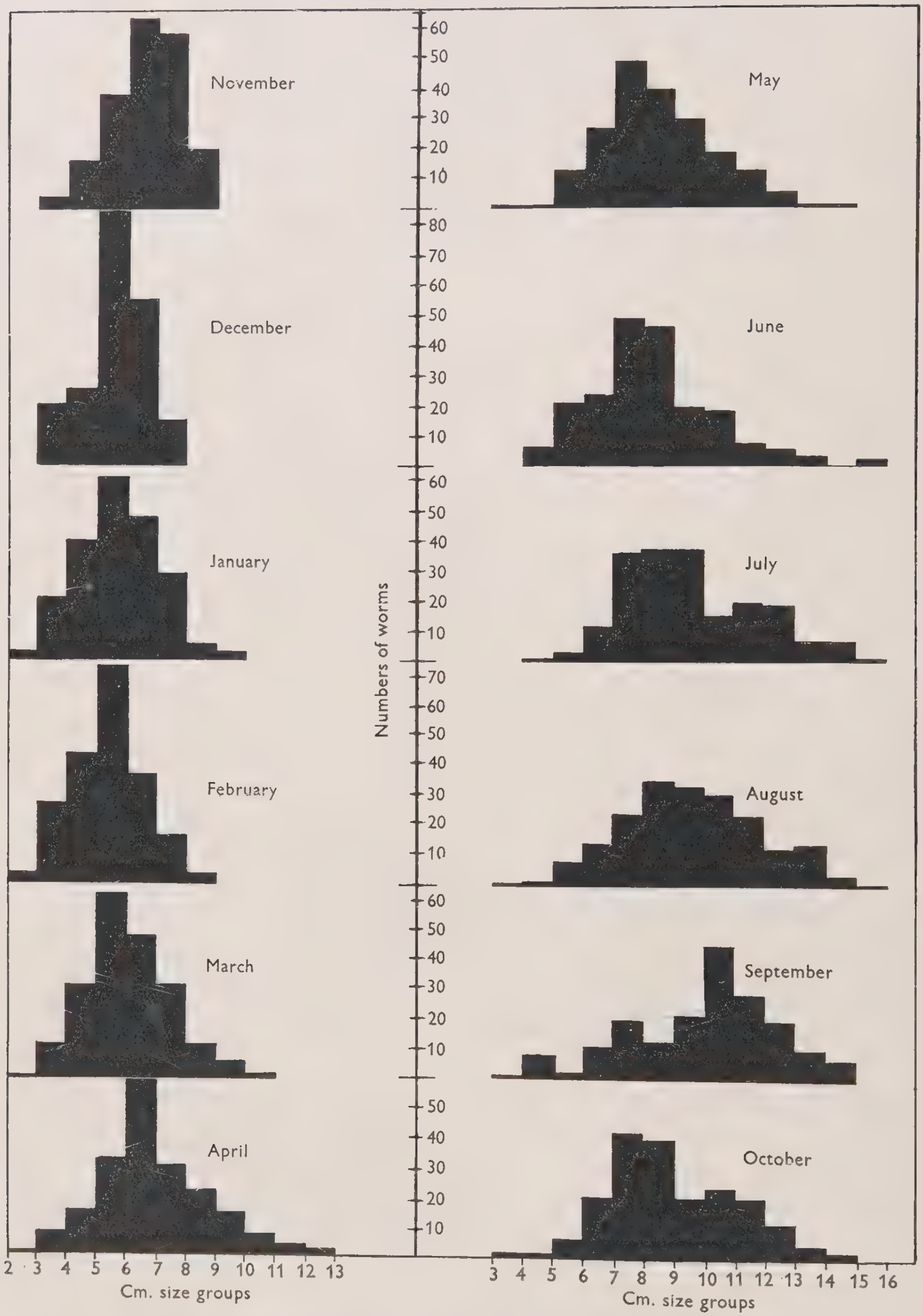

Fig. 12. Histograms showing numbers of worms in size groups differing by 1 cm. in length, November 1946 to October 1947.

following spring (April and May) the young worms which had attained a length index of 4 cm. in the previous September will have grown to a size which lies within the range of the adult size groups. Reference to Table I shows that in the autumn 98 % of the worms contain ripe germ cells so that it is clear that worms become sexually mature in their second summer and spawn 2 years after hatching from the egg. They can certainly spawn more than once, but how many times in not certain.

The histograms show a gradual change in the proportion of the various size groups. During the winter from December to March the 5–6 cm. group is the largest; in April it is the 6–7 cm.; in May the 7–8 cm. group is the largest; whilst in June the 7–8 and 8–9 cm. groups are about equal in size. By July the 7–10 cm. groups predominate and the 8–11 cm. in August. In September the 10–11 cm. group is the largest, but after October even worms exceeding 9 cm. in length are rare, whereas from May to October worms with a length index of up to 16 cm. are found. Now it has already been mentioned (p. 564) that at the end of October and during the first week of November there is evidence of a mortality of about 40 % of the adult worms. From the histograms it looks extremely probable that the worms which die are those in the larger size groups, that is, of 10 cm. and above. These presumably would be those which had reached a maximum size and had spawned for the last time. It will be seen that the size groups of 10 cm. and upwards for October represent about 37 % of the total—a figure which agrees well with the loss of 40 % estimated by another method.

This explanation is, however, inadequate to account completely for the decrease in size of the worms during the late autumn and winter. It can be seen that whilst the young (1946) worms grew steadily until September, yet from this time onwards they show a slight decrease in size. The same is true for the older worms as is shown by the decrease in average length from November to February. It seems that there is a period of 'degrowth' possibly due to the exhaustion of spawning and perhaps also because food is scarce at this time of the year. In this connexion I am indebted to Mr Wells for drawing my attention to the fact that lugworms kept in sea water alone remain alive and in good condition for long periods but become gradually smaller.

Migrations

Often regarded as an extremely sluggish animal, the lugworm is more active than is commonly supposed. It was repeatedly noticed that at all seasons of the year areas of soil from which all, or practically all, the worms had been removed by digging had been repopulated in the course of a few days to a normal density. It is possible that this repopulation was brought about by worms burrowing through the soil, but there is some evidence that worms leave their burrows when they are covered by the tide and swim to new situations and make fresh burrows. It has been noted that they can disappear into the soil quite rapidly, in fact, in about 3–4 min. (Chapman & Newell, 1947). On many occasions worms have been seen swimming in the aquarium, whilst reports of this occurring in nature have already been mentioned (p. 556). It may be suggested that worms captured when free-swimming are in fact merely migrating to new burrows, and that this may take place quite independently of spawning or the season of the year. Thus Meek & Storrow (1924) found swimming lugworms in March, and yet Storrow (1925) brought forward strong evidence that the breeding season was in September.

A simple experiment carried out in the autumn of 1947 provides yet further evidence that the worms can and do swim under natural conditions. A bucket was filled with soil and partially buried in the Flats so that a few inches of its rim projected above the surface. Some weeks later it contained an active adult worm which must have come in over the top of the bucket and could have done so only by swimming when the tide was up since lugworms seem unable to crawl on the surface.

The occurrence of post-larval stages in the spring plankton would then perhaps be best explained neither as accidental (Thorson, 1946) nor as the end product of a very extended pelagic larval phase (Blegvad, 1923; Thamdrup, 1935), but as short migrations to places suitable for the continuation of the adult mode of life.

Whatever may be the normal method by which lugworms change the location of their burrows, it seems that this is a normal and often repeated process, and is responsible for the distribution of the animals throughout the habitat. It is, perhaps, of particular importance to the worms of less than a year old. These are first detectable in the spring (April in 1947) by the enormous numbers of minute castings along the shoreward edge of the *Fucus* zone where there may be as many as 250 per sq. yd. Here the small worms grow rapidly and then gradually migrate away from the shore to mingle with worms spawned in previous years.

SUMMARY

The breeding season of the lugworms of the Whitstable area is a sharply defined one, extending for 14 days between the new moon and full moon spring tides in the second half of October. Spawning begins slowly and reaches a maximum at the intervening neap tides and then declines in intensity.

Both eggs and sperms are discharged from the burrows at extreme low water to lie on the surface of the sand. Here fertilization occurs.

No germ cells were detected in the body cavity from November to June, but from August onwards to the end of October 98 % of the adult worms are ripe.

At the end of the spawning period about 40 % of the adults die.

A brief description of gametogenesis and of the mature gametes is given.

Germ cells are discharged through the nephridia.

There is a differential sex ratio of 3·75 females to 1 male.

Coelomic gametes cannot be used for a completely successful artificial insemination, the eggs always dying after undergoing a few cleavages.

Fertilization and cleavage are briefly described. The eggs are fertilized as primary oocytes and undergo spiral cleavage in the way described by Child and others for different species of *Arenicola.*

Four to five days after fertilization the larva hatches. It is a very opaque trochophore 0·24 mm. long and usually rests sticking to the substratum, although it can swim actively. It has a broad prototroch, a telotroch and a mid-ventral tract of shorter cilia. There is an apical tuft and a pair of dark brown eyes. Mouth and anus do not seem to be open at this stage.

Larvae of about 14 days old and 0·25 mm. in length, and having two chaetigerous segments, are described. They were abundant in the silt between the pebbles of the *Fucus* zone, but no larvae were taken in the plankton nor in the sand of the Flats in which the adults spawned. It is suggested that fertilized eggs and larvae are carried inshore by the tide and are deposited in the *Fucus* zone where they live and develop into small worms in the winter and early spring of the following year. There is no extended pelagic larval phase, the modified trochophore larvae being demersal from the first.

Tables and graphs showing the growth of the young worms are given. The length of the body, excluding the tail, is taken as giving a true index of total length. The young worms hatched in 1946 were first noticed in April 1947 and by September had attained a length index of 4·3 cm.

The average length of the body, excluding the tail, for adults is also given in tabular and graphic form. This reaches its maximum (9·8 cm.) in September, but declines rapidly at the end of October and early November to the low level of about 5 or 6 cm. through the winter to rise again in the following spring.

From the histograms showing the numbers of worms in size groups differing by 1 cm. in length it is concluded that the sudden decrease in average length of the adult population at the end of October and early November is due to a mortality of adult worms (already mentioned) which have spawned for the last time. Worms spawn for the first time when they are 2 years old.

Further decrease in average length during the winter is due to other causes and affects the young as well as the adult worms.

Evidence is brought forward for the view that lugworms sometimes leave their burrows and swim for short distances probably to seek situations for new burrows. This kind of migration may be responsible for dispersing the animals throughout the habitat and accounts for its repopulation by young worms from the edge of the *Fucus* zone.

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THE GENERA *APOMATUS* AND *PROTULA* (POLYCHAETA, SERPULIDAE)

By Jean Hanson

Bedford College, University of London

(Text-fig. 1)

During an investigation of the blood systems of serpulids I have found that the pattern of the superficial blood vessels on the ventral surface of the thorax of the larger forms is a useful character for distinguishing the different genera, and sometimes is a reliable feature for distinguishing between the different species of a genus (e.g. *Serpula* and *Protula*). These blood vessels can easily be seen in living animals and are also visible in formalin-preserved specimens. Details of this matter will be published elsewhere.

Meanwhile, I wish to comment on the taxonomy of the genera *Apomatus* and *Protula*. The four western European species of these genera were obtained in the Gulf of Naples, and it was found that *Apomatus ampulliferus* Philippi, *A. similis* Marion and Bobretzky, and *Protula tubularia* (Montagu) all have the same type of superficial ventral thoracic blood system, whereas *P. intestinum* (Lamarck) is strikingly different in this respect. In *P. intestinum* (Fig. 1A) the trans-septal vessels (*tsv*) extend over the surface of the thorax and join the ventral vessel (*vv*); the vessels supplying the postero-ventral flange (*pvf*) of the thoracic membrane (*tm*) arise from the ventral vessel; the ventral vessel gives off other small vessels on to the surface of the thorax. In *P. tubularia*, *Apomatus similis* and *A. ampulliferus* (Fig. 1, B, C, D) the trans-septal vessels enter two ventro-lateral vessels (*vlv*) which terminate posteriorly in the flange of the thoracic membrane; the superficial blood system does not communicate with the ventral vessel. When specimens of these three species are handled they give off a strong odour which has never been encountered in *P. intestinum*; it resembles a mixture of machine-oil, oranges and iodine.

By taxonomists (e.g. Fauvel, 1927) the two genera are separated from each other by the presence of opercula in *Apomatus* and their absence in *Protula*. The most reliable feature distinguishing respectively *Apomatus similis* from *A. ampulliferus* and *Protula intestinum* from *P. tubularia* is the shape of certain adbominal chaetae. However, *Apomatus similis* has the same type of abdominal chaetae as *Protula tubularia*, and *Apomatus ampulliferus* has the same type of abdominal chaetae as *Protula intestinum*. The branchial crowns of these four species are readily autotomized when the animals are handled. When the crown with its opercula is lost *Apomatus similis* is indistinguishable from *Protula tubularia*; but the characteristic blood system of *P. intestinum* makes it easy to distinguish from *Apomatus ampulliferus*. On two occasions I have found apparently intact specimens of *A. ampulliferus* without opercula. They were distinguishable from *Protula tubularia* by their abdominal chaetae and from *P. intestinum* by their ventral thoracic blood systems. Thus it seems necessary to reconsider the validity of using the operculum as the diagnostic character for separating the operculate genus *Apomatus* from the non-operculate genus *Protula*.

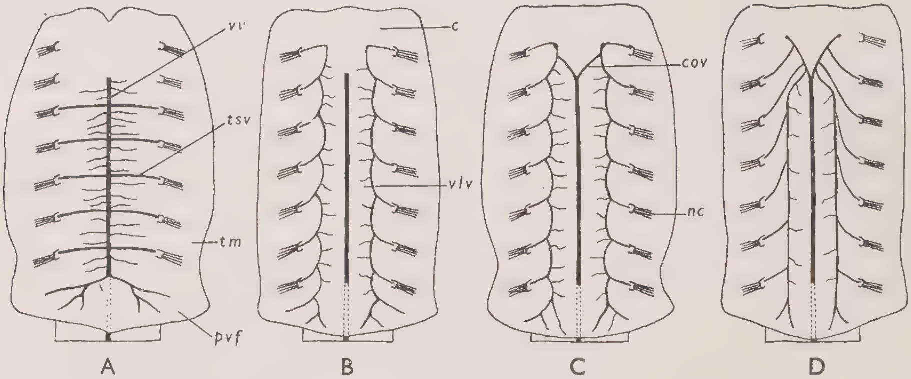

Fig. 1. Diagrams of superficial blood vessels on ventral surface of thorax. The collar has been turned forward. A, *Protula intestinum*; B, *P. tubularia*; C, *Apomatus similis*; D, *A. ampulliferus*. *c*, collar; *cov*, circum-oesophageal vessel; *nc*, notopodial chaetae; *pvf*, postero-ventral flange of thoracic membrane; *tm*, thoracic membrane; *tsv*, trans-septal vessel; *vlv*, ventro-lateral vessel; *vv*, ventral vessel.

The serpulid operculum and its peduncle represent a modified branchial filament. As Zeleny (1905) has shown, the existing serpulids can be arranged in a series reflecting the probable course of evolution of the operculum and its peduncle.

(i) Forms such as *Protula* without an operculum.

(ii) *Salmacina dysteri* with swollen tips to all its filaments. (Faulkner (1930) found that in her material the tips of the filaments were variable, some, none or all being swollen.) Similar swollen tips are noticeable on the filaments of the operculate species *Vermiliopsis infundibulum* (Philippi) and of the sabellid *Jasmineira candela* (Grube).

(iii) Forms such as *Filograna implexa* with two equally well-developed opercula, and *Apomatus* with a functional and a reserve operculum, all borne by filaments which in all other respects are just like non-operculate filaments.

(iv) Forms like *Pomatoceros* and *Hydroides* with one operculum, or with a functional and a reserve operculum borne by peduncles which are devoid of pinnules.

This series suggests that in the genera *Apomatus* and *Filograna* the filaments bearing opercula are in the process of evolving from ordinary branchial filaments. Hence less importance should be attached to the presence or absence of an operculum in the genera at the base of the series (*Protula*, *Apomatus*, *Salmacina*, *Filograna*) than in the genera later in the series (the rest of the serpulids). In the latter group of serpulids differences in opercular structure are accompanied by differences in other features and the opercula can satisfactorily be used for distinguishing genera. Within the former group of serpulids, however, *Apomatus* closely resembles *Protula*, and *Filograna* closely resembles *Salmacina* in most features, except that *Apomatus* and *Filograna* possess opercula whilst *Protula* and *Salmacina* do not. I suggest that a more natural scheme of classification would be obtained by combining *Apomatus* and *Protula* into one genus, and *Filograna* and *Salmacina* into another genus.

I suggest also that the genera *Apomatus* and *Protula* should be revised to reflect the close similarity between *P. tubularia* and the two species of *Apomatus*, and the dissimilarity of *Protula intestinum*. Fauvel (1927) has already commented on the similarity of *Apomatus similis* and *Protula tubularia* and has suggested that the former might be a young form of the latter. On the French coast (Fauvel, 1927) *Apomatus similis* is smaller than *Protula tubularia*; at Naples also this was usually so, but I found two specimens of *Apomatus similis* of the same size as *Protula tubularia*.[1]

The taxonomy of *Salmacina* and *Filograna* is similarly in need of revision. Faulkner (1930) has noticed operculum-like swellings at the tips of some or all of the non-operculate filaments of some specimens of *F. implexa* and *Salmacina dysteri*, and has agreed with McIntosh (1922–23) that the separation of the operculate genus *Filograna* from the non-operculate genus *Salmacina* is unsatisfactory, because in other respects they are closely similar. Faulkner considers that *Filograna implexa* and *Salmacina incrustans* are identical except that the former possesses opercula. According to Fauvel (1927), *Filograna* is bisexual, thus differing from *Salmacina* which may be hermaphrodite; but Faulkner has found hermaphrodite specimens of *Filograna implexa*.

I wish to thank the staff of the Zoological Station of Naples, the British Association for the Advancement of Science for the use of its Table, and the University of London for a grant towards travelling expenses.

SUMMARY

It is suggested that the genera *Apomatus* and *Protula* should be revised to reflect the close similarity between *P. tubularia* and the two species of *Apomatus*, and the dissimilarity of *Protula intestinum*. It is further suggested

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[1] McIntosh (1922–23) suggests that there is only one species of *Apomatus* (*A. ampulliferus*) and only one species of *Protula* (*P. tubularia*).

that the presence or absence of an operculum is not a sufficiently important character for distinguishing *Apomatus* from *Protula*, or *Filograna* from *Salmanica*; and therefore that these two pairs of genera should be fused into two genera.

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CLEANSING MECHANISMS AND THE FUNCTION OF THE FOURTH PALLIAL APERTURE IN *SPISULA SUBTRUNCATA* (DA COSTA) AND *LUTRARIA LUTRARIA* (L.)

By C. M. Yonge, F.R.S.

From the Marine Biological Station, Millport, and the Department of Zoology,
University of Glasgow

(Text-figs. 1–8)

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INTRODUCTION

The investigations here recorded were the outcome of a preliminary study of *Lutraria lutraria* (L.) in connexion with a wider study on adaptation for deep burrowing in Lamellibranchiata. Examination of the ciliary currents concerned with the removal of waste material from the mantle cavity, which involved inquiry into the function of the fourth pallial aperture, revealed a variety of unrecorded facts. This led to an examination of conditions in *Spisula subtruncata* (da Costa) with which, on the basis of hinge characters, *Lutraria* is grouped in the family Mactridae (Thiele, 1935). Additional evidence of the close relationship between these two genera has been found.

This work was carried out at the Millport Laboratory, and it is a pleasure to record the kindness and help given by the Director, Mr R. Elmhirst, and by other members of the Staff. Thanks are also due to Dr H. F. Steedman for the preparation of sections.

SPISULA SUBTRUNCATA

External Appearance and Habits

Spisula subtruncata is a stoutly built bivalve which inhabits silty sand, into which it burrows quickly by means of a thick, somewhat pointed foot. The siphons (Figs. 1 and 2) are united and, in a specimen 3·4 cm. long by 2·6 cm. deep, extend to a length of not more than 8 mm., usually somewhat less. When buried only their tips project above the surface. The fused siphons are surrounded by a sheath of periostracum which arises in a groove immediately anterior to the outer ring of tentacles. The siphons thus represent the fusion of the inner and middle lobes, with the marginal (periostracal) groove of the outer lobe, of the mantle edge (Yonge, 1948). The middle (sensory) lobe is represented by a ring of tentacles which surrounds both siphons (Fig. 2). The inner (muscular) lobe is represented by a ring of large, with intermingled small, tentacles round the opening of the inhalant siphon, and by a membrane round that of the exhalant siphon. These tentacles are very mobile and act as strainers, preventing large particles from entering with the inhalant current, while the membrane constricts and directs the exhalant current.

When the adductors relax, the ventral margins of the shell valves separate for a distance of about 2 mm., but the mantle lobes remain closely applied as shown in Fig. 1. They are actually free from the region of the anterior adductor to the base of the siphons, so providing an exceptionally long pedal opening. But this only functions when the foot is protruded; at other times the ventral surface is closed, except for a small area immediately posterior to the fusion of the mantle edges at the base of the siphons. Here a spherical opening, about 1–2 mm. in diameter, can be seen when the animal is expanded (Figs. 1 and 2, MA). Similar local separation of the mantle edges in this region was originally noted by Kellogg (1915) in *Mactra solidissima* Dilwyn.

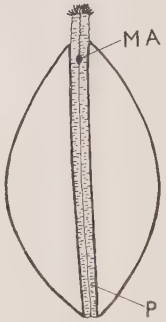

Fig. 1. *Spisula subtruncata*, animal fully expanded viewed from ventral surface. × 1. MA, mantle aperture, margins fused on posterior side only; P, periostracum covering exposed mantle surfaces and siphons.

The Mantle Cavity

The appearance of the organs in the mantle cavity after removal of the right shell valve and mantle lobe is shown in Fig. 2. The flat and homorhabdic gills are large with the outer only about half the size of the inner demibranch. Their ciliation has been described by Atkins (1937 *a*, *b*). Small frontal cilia beat ventrally, carrying material into the marginal food grooves, except on the inner surface of the outer demibranch where they beat towards the gill axis.

But on this and on the adjacent surface of the inner demibranch there are additional long coarse frontal cilia which beat ventrally so that all large particles, such as sand grains, are carried into the food grooves, out of which they fall on to the surface of the mantle for extrusion with other waste material. Atkins associates the presence of these large cilia, which she notes are fully active only on mechanical stimulation, with life in silty sand. By their means many of the larger particles are removed from the gills, but mucus-laden strings of finer particles reach the long, strap-shaped palps by way of the food grooves and the gill axis. The palps function in the usual manner, further selection by them leading to the rejection of larger particles and masses from their tips.

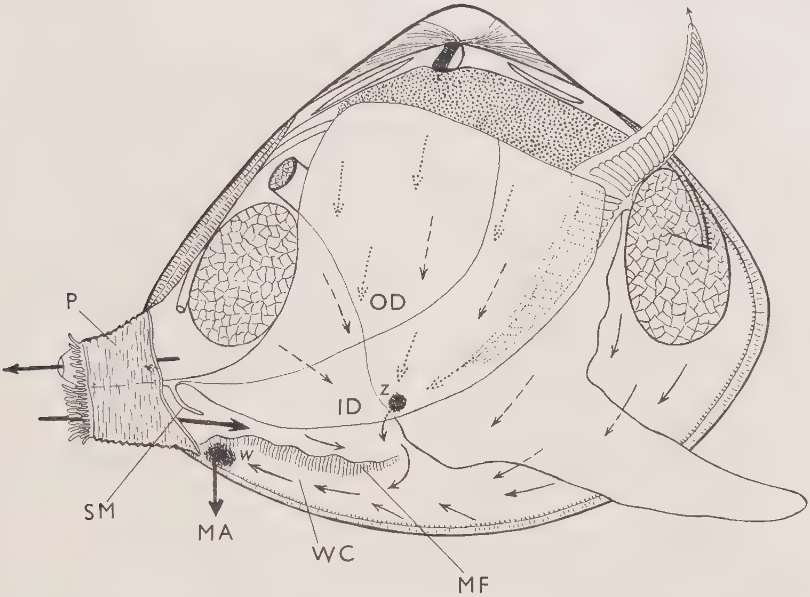

Fig. 2. *Spisula subtruncata*, animal viewed from right side after removal of right shell valve and mantle lobe, siphons intact. $\times 2\frac{1}{2}$. ID, inner demibranch; MA, mantle aperture with arrow showing direction in which waste (*w*) ejected; MF, mantle fold (left); OD, outer demibranch; P, periostracum surrounding siphons; SM, siphonal membrane; WC, waste canal; *z*, temporary accumulation of waste on visceral mass at base of the foot. Solid and broken arrows indicate course of ciliary currents on mantle (exposed or beneath other organs), dotted arrows currents on visceral mass. Currents on gills and palps (apart from rejection from tips of latter) not shown.

On the posterior third of the mantle surface a pair of horizontally extending mantle folds (Fig. 2, MF) form, by apposition, a roof over the applied mantle edges. Similar folds have been described by Kellogg (1915) in three other species of Mactridae, *Schizothaerus nuttalli* (Conrad), *Mactra solidissima* Dilwyn and *Spisula polynyma* Stimpson, although not in *S. planulata* (Conrad). Somewhat similar folds occur in various deposit-feeding Lamellibranchiata, species of *Scrobicularia*, *Abra* and *Macoma*, but they have a somewhat different function. From the roof of the inner opening of the inhalant siphon a flap or siphonal membrane (Kellogg) hangs down (Fig. 2, SM). This, as shown below, is probably associated functionally with the mantle folds.

Removal of Waste Material

All currents on the mantle surface and visceral mass, but *not* on the gills, are shown in Fig. 2. The foot, as usual, is not ciliated. On the visceral mass the cilia (dotted arrows) carry material to an area (*z*) behind the posterior margin of the foot, which also receives matter rejected from the inner palps. On the mantle surface ciliary currents (broken and solid arrows) converge mid-ventrally posterior to the foot and at the entrance to the ventral tract, termed 'waste canal' by Kellogg, which is roofed by the mantle folds. The accumulated waste from the visceral mass and palps also passes into this canal in which all material is carried posteriorly.

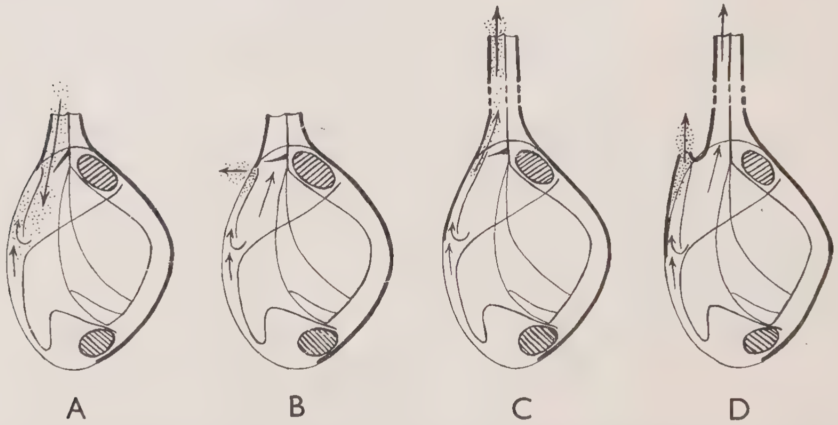

Fig. 3. Diagrammatical representations of cleansing mechanisms in various Mactridae. Extent of mantle fusion indicated by thickened outline. A, *Spisula subtruncata*, intake of sediment with inhalant current, showing action of siphonal membrane and passage of waste into canal guarded by mantle folds; B, *S. subtruncata*, ejection of waste ventrally through mantle aperture; C, *Schizothaerus nuttalli*, ejection of waste posteriorly through inhalant siphon owing to backward extension of waste canal behind siphonal membrane (based on Kellogg); D, *Lutraria lutraria*, ejection of waste posteriorly through fourth pallial aperture, mantle folds but *not* siphonal membrane being retained.

The siphonal membrane opens inward and so offers no resistance to the inflowing current. Kellogg suggests that 'its function is to throw the current downward on to the mantle edges, and away from the gills, when much sediment is present'. This view, implying that the membrane is an adaptation for life in silty water, appears correct. This deflexion of the water current necessitates some means of preventing the accumulation of waste at the base of the siphon from being swept forward. This, as Kellogg points out, explains the presence of the mantle folds which over-arch the waste canal. The action of both the membrane and the folds is shown diagrammatically in Fig. 3 A, B.

In *Schizothaerus nuttalli* the mantle edges, as Kellogg has shown, are fused as far forward as the anterior end of the mantle folds (see Fig. 3 C). But here the mantle folds and the waste canal terminate *behind* the siphonal membrane so that when the adductors contract for cleansing, the accumulated waste is ejected through the long inhalant siphon in the usual manner (Fig. 3 C). This animal, the Pacific horse-clam or gaper, is one of the largest of lamellibranchs, with a shell attaining a length of 8 and a breadth of 5 in. The fused siphons, encased in periostracum as in all Mactridae, are very long so that the animal often occurs at depths of up to 2 ft. or over (Quayle, 1941). But in the shallow burrowers, such as *S. subtruncata* and, judging from Kellogg's figure, in *S. polynyma*, these folds terminate, and the waste accumulates, *in front of* the membrane as shown in Fig. 2. This would appear to explain the local separation of the mantle edges in this region in *S. subtruncata*. Kellogg makes no mention of a similar opening in *S. polynyma*, but his account of this species is brief. In the former species a slow current of water is drawn in through this opening when the adductors are relaxed, but when they contract the waste is ejected through it. Back pressure of water will drive the siphonal membrane back and largely, if not completely, block the lumen of the siphon. The differences between this condition and that described by Kellogg in *Schizothaerus* are indicated in Fig. 3 B and C.

Conditions are somewhat different in *Mactra solidissima*, where Kellogg found that cilia and muscle combine to remove the waste ventrally. In the unrelated *Cardium corbis* Martyn all waste matter is so removed by ciliary action alone. In neither of these species is the posterior end of the animal buried, and this method of cleansing represents, Kellogg states, 'the usual procedure in forms with free mantle margins, and which are not completely buried in a burrow'. Waste could certainly not be removed ventrally by ciliary action in *Spisula subtruncata* which is completely covered with sand when it burrows.

The expulsion of waste ventrally following contraction of the adductors in *S. subtruncata* thus involves the presence of what is in effect, if not structurally, a fourth pallial aperture. This gives the key to the explanation of conditions here for the first time fully described in *Lutraria lutraria*.

LUTRARIA LUTRARIA

External Appearance and Habits

Lutraria lutraria (Fig. 4) is adapted for deep burrowing usually in rather shifting sands, although it also lives in mud where this is overlaid with sand. It occurs on the shore near low water of spring tides and in the sublittoral zone. The large oval shell with a wide posterior gape closely resembles that of the other genera of deep-burrowing lamellibranchs, *Mya* and *Panope*. This resemblance is the result of convergence due to similarity of habits. Attention is here confined to the less obvious but fundamental relationship between *Lutraria lutraria* and the shallow burrowing species of the Mactridae, in particular *Spisula subtruncata*.

The shell attains a size of some 13 cm. long by 7 cm. broad. The massive, fused siphons extend for up to three times the length of the shell and, apart from their size, resemble in all respects those of *S. subtruncata*, being similarly covered with periostracum and fringed with tentacles and with a membrane round the exhalant siphon. There is also a true fourth pallial aperture. As shown in Fig. 4, the distended mantle edges extend for some distance beyond the margin of the shell and, at the base of the inhalant siphon, form a posteriorly directed papilla which marks the site of this aperture (FA).

The Mantle Cavity

The disposition of the organs when exposed by the removal of the right shell valve and mantle lobe is shown in Fig. 5. Compared with *S. subtruncata*, they are extended longitudinally, especially in the posterior half of the body. The visceral mass is large, but the foot, though big for a deep burrower, is relatively smaller than in that species. The pedal gape is confined to the anterio-ventral surface. The gills are large and the outer demibranch only a little smaller than the inner one. Atkins (1937 *b*) describes them as plicate and homorhabdic, and has shown that currents run oralward along the marginal food grooves and along the gill axis, as in *S. subtruncata*. The long frontal cilia found in that species are absent. The palps are large but broad at the base which approaches in length the two free margins.

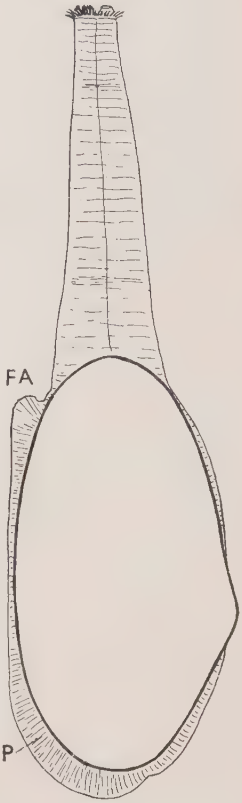

Fig. 4. *Lutraria lutraria*, fully expanded animal viewed from right side. ×½. FA, fourth pallial aperture; P, periostracum covering exposed mantle surfaces and siphons.

Between the wide pedal gape and the small fourth aperture, the mantle edges are fused for rather more than half the length of the ventral surface (between FA and PG). Atkins (1937 *c*) has shown that it is the cuticular linings of the applied epithelia that fuse, as shown in Fig. 8 (CF). She notes that, unlike *Ensis siliqua* (L.), *E. arcuatus* Jeffreys, and *Cultellus pellucidus* (Penn.), where cuticular fusion of the mantle edges also occurs, there is no rupture along the line of fusion when the animal dies and gapes widely. She thinks, therefore, that there may be fine cross-connecting strands of muscle in *Lutraria lutraria*. Owing to the folds into which the epithelia are thrown in fixation, she found it impossible to determine this matter in sections. However, when examining stocks of specimens that had been preserved for several years in formalin it was found that the fused surfaces had either come apart or could be separated with the greatest ease. The exposed surfaces were perfectly smooth with no trace of any ruptured tissues. Apparently long exposure to formalin softens the cuticle along the line of fusion and this represents the only means whereby the two lobes are united. But they are certainly fused much more firmly than in *Ensis* or *Cultellus*.

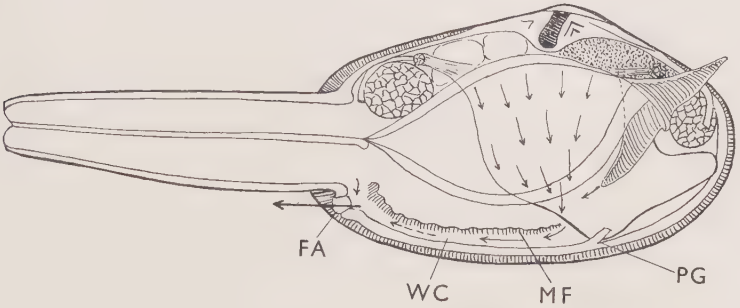

Fig. 5. *Lutraria lutraria*, animal viewed from right side after removal of right shell valve and mantle lobe, siphon cut longitudinally. × ½. PG, posterior end of pedal gape. Other lettering as before. Arrows indicate course of ciliary currents on the visceral mass and within the waste canal.

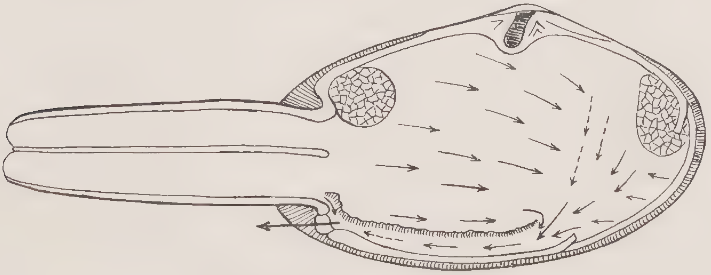

Fig. 6. *Lutraria lutraria*, as in Fig. 5, but with organs removed to expose the mantle surface and with arrows indicating the direction of the ciliary currents on this, weaker ones shown by broken arrows.

The fourth aperture is short, not more than 5 mm. long in an animal of shell length 11·5 cm. The mantle margins are here somewhat thicker, owing to a greater development of the pallial muscles. Well-developed mantle folds, shown in section in Fig. 8, extend from the base of the inhalant siphon, i.e. just posterior to the fourth aperture, to near the posterior margin of the foot and visceral mass, exactly as in *Spisula subtruncata* only for a relatively longer distance owing to the posterior extension of the body in *Lutraria lutraria*. There is no trace of a siphonal membrane.

Removal of Waste Material

The course of the ciliary currents on the visceral mass and of those on the surface of the mantle is shown in Figs. 5 and 6. On the former, material is carried ventrally to the posterior margin adjacent to the hinder surface of the foot. Conditions therefore resemble those in *Spisula subtruncata* and not in *Mya arenaria* L., where all currents beat towards vortices on either side of the posterior end of the more longitudinally extended visceral mass and nearly opposite the opening of the inhalant siphon (Kellogg, 1915; Yonge, 1923). There are no vortices in *Lutraria lutraria*, the accumulated waste material passing off the visceral mass to enter the posterior end of the waste canal (Fig. 5). On the mantle surface also, the direction of the ciliary currents is essentially similar to that in *Spisula subtruncata*. Over the posterior two-thirds, particles are carried forward as far as the anterior margin of the currents on the visceral mass. Here weak, ventrally directed, currents convey them to the entrance of the waste canal. Currents around the margin of the wide pedal gape carry material to the same point. In *Mya*, where the currents are more powerful, all material is carried into vortices, one on each side of the posterior end of the pedal gape.

The currents in the waste canal, when viewed from above with the mantle folds drawn apart, are shown in Fig. 7. All waste, as shown above, enters this canal. There are no cilia along the mid-line, where the cuticular surfaces of the mantle edges fuse. This is also true of the flaps which fringe the pedal gape and the fourth aperture. Two tracts of cilia (Fig. 8, *c*) are present on either side of the mid-line. The nearer ones, shown in Figs. 7 and 8, lie on the surface of a pair of low ridges. The others, only shown in the section (Fig. 8), are situated at the bases of the mantle folds. The greater part of the under surface of the folds is unciliated, but the ciliated epithelium which covers the general surface of the mantle extends over the upper face of the folds and for a short distance over their margins on to the under surface (Fig. 8). Subepithelial mucous glands, indicated diagrammatically in Fig. 8, are associated with all ciliated areas. The unciliated epithelium is much lower and almost devoid of glands.

Within the anterior half of the canal particles travel back with some speed, but behind this, in the region indicated by the broken arrows, the currents are very weak. More powerful currents exist between the base of the inhalant siphon and the fourth aperture towards which they carry particles. Conditions are thus very different from those in *Mya*. There an exceptionally powerful posteriorly beating tract of cilia occupies a broad mid-ventral area formed by the complete fusion of the mantle edges. Elongated areas of mucous cells on either side of the pedal opening (originally described by Vlès, 1909) supply mucus in which the waste particles are consolidated in masses at the base of the inhalant siphon through which they are periodically ejected. No such glandular areas are present in *Lutraria lutraria*.

The necessity for removing waste must be no less in *Lutraria* than in *Mya*, but the mechanism is certainly different. When fully expanded, as shown in Fig. 4, the fourth aperture is normally closed. But the immediate effect of contraction by the locally enlarged pallial muscles, which accompanies that of the adductors, is to pull the lips apart so that a longitudinal slit is converted into a circular opening. As already noted, this points posteriorly and is in line with the waste canal. Hence all material within this will be ejected through the fourth aperture. Bloomer (1903) noted that *Lutraria* uses this 'aperture frequently in suddenly ejecting water or any objectionable matter from the pedal cavity'. Atkins (1937 *c*) agrees with him. Neither, however, notes the presence of the pallial folds. The absence of a siphonal membrane in *Lutraria*, possibly correlated with the less silty environment, enables the greater part of

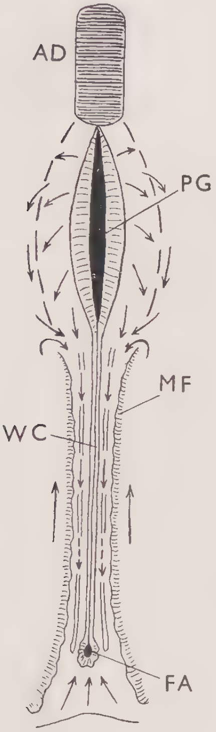

Fig. 7.

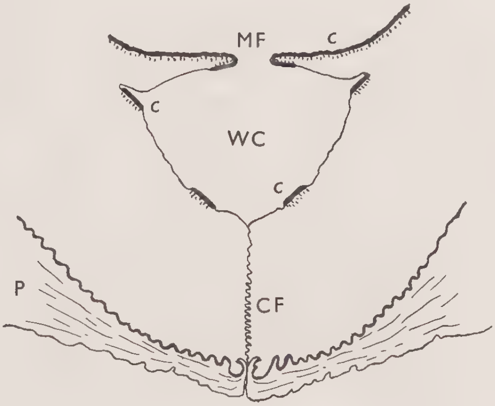

Fig. 8.

Fig. 7. *Lutraria lutraria*, mid-ventral region of the mantle viewed from above. $\times \frac{3}{4}$. AD, anterior adductor; PG, pedal gape. Other lettering as before. Arrows indicate direction of ciliary currents carrying material to fourth aperture.

Fig. 8. *Lutraria lutraria*, semi-diagrammatic drawing of section through the fused mantle edges and waste canal. $\times 2$. *c*, areas of ciliated epithelium with underlying mucous glands; CF, cuticular fusion of mantle edges. Other lettering as before.

the water in the large inhalant chamber to be expelled at the same time through the inhalant siphon, as in the even larger *Schizothaerus* where the waste is carried out by this route. In Fig. 3 D conditions in *Lutraria* are shown diagrammatically in comparison with those in *Spisula subtruncata* and in *Schizothaerus*.

DISCUSSION

It would appear from the foregoing account that a siphonal membrane has evolved in shallow-burrowing Mactridae, such as *Spisula subtruncata* and *S. polynyma*, as an adaptation to life in silty water. The long frontal cilia on the gills of the former, described by Atkins (1937 *a*, *b*), represent a further adaptation to these conditions. The protection of the waste canal by mantle folds is correlated initially with the presence of the siphonal membrane, as postulated by Kellogg. Where the hind end of the shell is not covered when the animal burrows, as in *Mactra solidissima*, ciliary currents may be adequate to remove the waste ventrally from the canal. But in *S. subtruncata*, where the entire shell is covered, muscular means are needed, and correlated with this the mantle edges separate locally at the base of the siphons, providing an aperture through which waste is periodically expelled ventrally.

An interesting contrast is provided by the two deep-burrowing genera, *Schizothaerus* and *Lutraria*. In both long siphons are formed while the mantle edges fuse over the posterior half of the ventral surface. But in *Schizothaerus*, which possibly lives under more silty conditions, the siphonal membrane is retained. Fusion of the mantle edges renders ventral ejection of waste impossible, but the posterior extension of the mantle folds and waste canal behind the siphonal membrane enables waste to be carried out through the inhalant siphon. In *Lutraria*, on the other hand, there are no long frontal cilia and no siphonal membrane, both associated with life in silty water, but the mantle folds, probably originally acquired in association with the membrane, remain. They retain their function because a true fourth aperture is present which, owing to the protrusion of the mantle edges, is directed posteriorly. The waste is thus expelled along a passage parallel to, but owing to the intervention of the mantle folds distinct from, the inhalant siphon. Owing to its descent from some form not unlike *Spisula subtruncata*, the cleansing mechanisms of *Lutraria* are very unlike those of *Mya*, despite the similarity of external form and of habit in the two genera.

A fourth aperture is present in a number of other Lamellibranchiata, in species of *Ensis* and *Cultellus pellucidus* and in many of the Anatinacea (Pelseneer, 1890, 1911). The nature of the opening in the former has been discussed by Bloomer (1903), Graham (1931) and Atkins (1937 *c*). In *Ensis* it lies in about the middle of the ventral surface, in *Cultellus* it is more anterior. The mantle edges between the fourth and pedal apertures are united only by cuticular fusion (Atkins, 1937 *c*), and very readily separate when the animals are removed from the sand or mud which normally presses against the shell valves. Atkins considers that the function of the fourth aperture in these animals is to act 'normally as an additional inhalant aperture, and, on sudden closure of the valves, for ejection of unwanted particles'. The former function can be at best merely incidental; any opening into the inhalant cavity will admit water when the lateral cilia on the gills are beating. The same criticism can be made of the second function ascribed to it. Graham (1931) has shown that waste material is conveyed, in the usual manner, to the base of the inhalant siphon in *Ensis siliqua*. It appears more probable that the fourth aperture in these animals is essentially a safety valve which permits the ventral extrusion of some of the water in the mantle cavity when these rapidly burrowing animals make the sudden muscular contractions involved in downward movement. It is certainly not associated with special mechanisms concerned with collection of waste as it is in *Lutraria*.

In the Anatinacea the aperture lies, as in *Lutraria*, at or near the base of the inhalant siphon. The mantle edges are extensively fused along the ventral surface. Atkins (1937*c*) has shown that there is complete tissue fusion in *Thracia villosiuscula* F. & H., and this is probably true of all Anatinacea. Kellogg is the only worker to examine the mantle cavity in life, and he has shown that waste collects in the vicinity of the fourth aperture in *Mytilimeria nuttalli* (Conrad) and *Lyonsia saxicola* Baird. But there are no associated mantle folds, and he was unable to determine with certainty the significance of the opening. In the abyssal genera, *Asthenothaerus* and *Periploma*, Pelseneer (1911) describes a third ventral adductor immediately posterior to the fourth aperture. Such evidence as there is would therefore seem to indicate that the function of the fourth aperture in the Anatinacea is similar to that in *Lutraria*. But further study in life of species of this little-known group is needed.

SUMMARY

Spisula subtruncata is a shallow-burrowing member of the Mactridae which inhabits silty sand. Adaptations to such conditions include long frontal cilia on the gills (Atkins), and the presence of a siphonal membrane with associated mantle folds over-arching a waste canal, as postulated by Kellogg for allied species.

The mantle edges are free ventrally, but are normally closely applied except for a short distance at the base of the inhalant siphon, an effective fourth pallial aperture being so formed. Through this opening material from the waste canal is ejected.

Lutraria lutraria is a deep-burrowing species belonging to the same family. The general resemblance to *Mya arenaria* is due to convergence. Cleansing currents resemble those of *Spisula subtruncata* and there is a similar waste canal, but the siphonal membrane and the long frontal cilia associated with a silty environment are absent.

The mantle edges are firmly united along the posterior half of the ventral surface by fusion of the bounding cuticle (Atkins), but there is a true morphological fourth aperture at the base of the inhalant siphon. This is directed posteriorly and all waste is probably ejected through it.

Schizothaerus nuttalli, described by Kellogg, is another deep-burrowing member of the Mactridae, but here the mantle edges are fused without leaving a fourth aperture. Waste is ejected through the inhalant siphon owing to the extension behind the siphonal membrane of the waste canal and mantle folds.

It is suggested that the fourth aperture in species of *Ensis* and *Cultellus* acts as a safety valve through which some of the water leaves the mantle cavity following the sudden contractions which occur in these rapidly burrowing species.

The fourth aperture in many Anatinacea has never been adequately studied. Existing data indicate that it may be concerned with the ejection of waste, but there is no associated waste canal with mantle folds.

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THE STRUCTURE AND LIFE HISTORY OF SOME MINUTE PROSOBRANCHS OF ROCK POOLS: *SKENEOPSIS PLANORBIS* (FABRICIUS), *OMALOGYRA ATOMUS* (PHILIPPI), *RISSOELLA DIAPHANA* (ALDER) AND *RISSOELLA OPALINA* (JEFFREYS)

By Vera Fretter, Ph.D.

From the Department of Zoology, Birkbeck College, University of London

(Plate IV and Text-figs. 1–6)

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INTRODUCTION

Amongst the more common inhabitants of the seashore are a number of prosobranch molluscs which, owing to the smallness of their size, have escaped investigation. *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *R. opalina* (Jeffreys) are some of the least known of these: their shells, and so much of their body as is exposed when the animal is creeping, have been described by Forbes & Hanley (1853) and Jeffreys (1867), but the internal anatomy and most of their habits are entirely unknown. The present investigation shows that in many respects these molluscs are highly specialized in correlation with their small size and their habitat. The more important features of structure and life history are described for each animal and, in the discussion, the features which they share because of their minuteness and their adaptation to a rock-pool habitat are dealt with.

SKENEOPSIS PLANORBIS (FABRICIUS)

Skeneopsis is found abundantly all around the British Isles and is especially plentiful in coralline pools. The shell is roughly discoidal in shape, having an extremely depressed, blunt and rounded spire which is scarcely visible unless the shell be viewed edge-on (Fig. 1 A, B). There are four rather loosely coiled whorls, with deep sutures, and the umbilicus is open and funnel-shaped. The last whorl is by far the largest. The mouth is almost circular, its lips projecting outwards, thin and entire in young specimens, though somewhat flexuous in older ones looking as if an original entire edge had been clipped. The only sculpture on the shell is due to the lines of growth (LG). The colour varies: typically, as in young specimens, the shell is reddish brown and glossy; older specimens may be dull and either a pale buff or olive green owing to algal growth. As the mollusc grows to maturity algal spores gain a holdfast on the surface of the shell. These germinate and the small plants become embedded in a thick layer of mucus which they themselves secrete, and the layer may be added to by diatoms which are scattered in large numbers amongst the algal filaments. Thus in older specimens the shell is completely encased in a mucous covering from which arises a thick woolly coat of algal filaments.

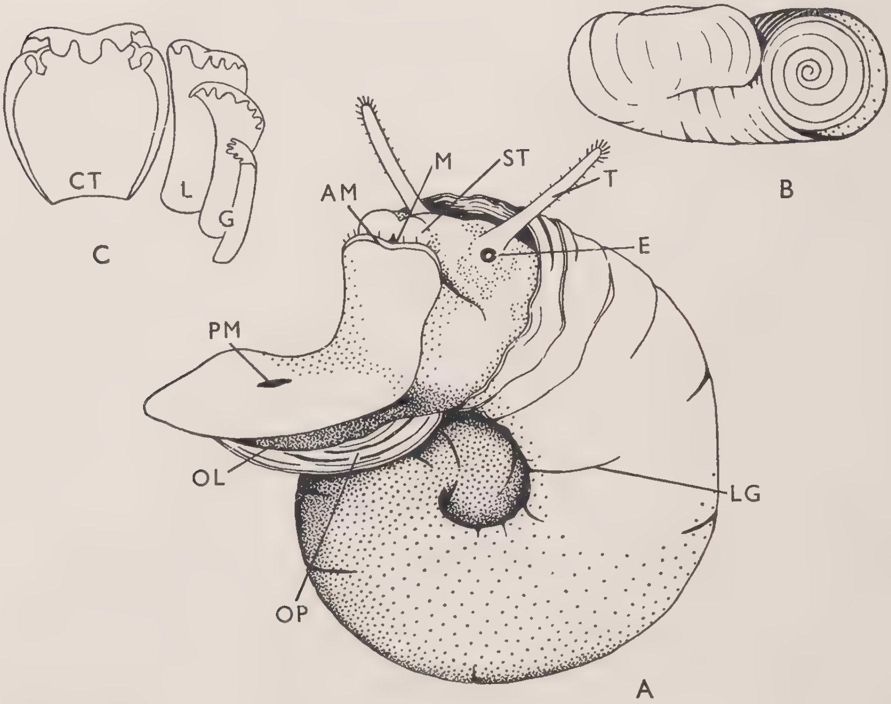

Fig. 1. *Skeneopsis planorbis*. A. Living animal seen from the left and below. ×45. B. Shell from the side. ×30. C. Half row of radula teeth. ×230. AM, opening of anterior pedal gland; CT, central tooth of radula; E, eye; G, marginal tooth of radula; L, lateral tooth of radula; LG, puckered lines of growth; M, mouth; OL, opercular lobe of foot; OP, operculum; PM, opening of posterior pedal gland; ST, snout; T, tentacle.

When *Skeneopsis* crawls over weed or rock the shell is not carried erect but tilted sideways and may be rocked from side to side. The exposed parts of the body have a ground colour of greyish white. On the metapodial (opercular) lobes (Fig. 1 and Pl. IV, fig. 1, OL) there is a mottling of deep grey or black, and patches of yellow occur on the body, all due to epithelial pigment granules. Two yellow patches lie between the eyes, each over a similarly pigmented region of the buccal cavity, with another of smaller size behind each eye, and a streak underlies the operculum. The two dorsal patches which lie close together are contiguous with a black streak extending for some distance beneath the shell. The head bears a pair of long cylindrical and widely diverging tentacles which may be waved slowly in the water as the mollusc creeps. Each is scantily covered with motionless cilia (Fig. 1, T), and the eye is situated on the outer side of the swollen base (E). The snout (ST) is broad with a mid-dorsal groove dividing it into two rounded lobes, between which lies ventrally the mouth (M). The foot is relatively short, truncated in front and tapering along the posterior third to a blunt point. Around the anterior edge a deep groove marks the opening of the anterior pedal mucous gland (AM), and a row of stiff cilia arises from the upper lip of the groove. The anterior pedal gland comprises three groups of mucous and mucoid cells set in a transverse row in the anterior tissues of the foot (Pl. IV, fig. 1, MG); the middle group is the most extensive, and the whole appears as a semicircular opaque white mass in the living animal. Gland cells of a similar nature are embedded in the tissues of the sole (GD) and open singly between the cells of the ciliated columnar epithelium. Yet another and still greater supply of mucus comes from a posterior pedal gland which opens as a mid-ventral longitudinal slit about a third of the pedal length from the posterior end (Fig. 1, PM). The opening leads dorsally into a ciliated duct (Pl. IV, fig. 1, D), which soon bifurcates into left and right branches, and each becomes surrounded by glandular tissue which extends into the haemocoel. On each side, at about the level of the pedal ganglia, this tissue then splits into two lobes, one passing dorsally (AL) and the other running back alongside the oesophagus and immediately above the columellar muscle (PL).

The animal is fond of crawling on the surface film of water and may suspend itself from this by means of a viscid thread issuing from the posterior pedal gland. The free end of the thread floats on the surface, and, as the animal slowly descends, it plays out the mucous rope: from the opening of the gland the secretion is directed into a longitudinal groove along the sole, where, in contact with the sea water, it hardens before leaving the posterior end of the foot. In such a manner *Skeneopsis* may finally reach the bottom of a shallow pool, or, if the thread be short, the mollusc may even reverse its course and climb along it to reach the surface again.

The mantle cavity extends along the whole length of the body whorl. On the left side is the well-developed, bipectinate osphradium, and dorsal to this the monopectinate gill, which has only nine finger-like filaments (Pl. IV, fig. 1, F) projecting downwards from a somewhat elongated axis. The hypobranchial gland runs along the right wall of the cavity anteriorly. It passes back parallel to, and just above, the rectum as a single layer of mucous and mucoid cells, but near the level of the posterior end of the ctenidium the gland thickens, occupies a more dorsal position and the mucus is replaced by another type of protein. Posteriorly, the mantle cavity is much reduced in size, and, covered by the hypobranchial gland, pushes back over the kidney (K), which therefore opens on its floor. In the female the large glandular genital duct projects from the right wall of the mantle and partly obliterates the cavity on this side, the rectum running along its median side to open on a prominent papilla anterior to the genital opening. In the male the genital duct is far less conspicuous, and the anal papilla smaller. The penis (PE), which arises behind the right tentacle, is slightly compressed laterally and when fully developed extends the whole length of the mantle cavity.

The Alimentary Canal

The mouth leads dorsally into a short though very dilatable tube, a ventral extension of the buccal cavity which bears a cuticle, and this also spreads on to the floor of the main part of the cavity in which the odontophore lies. At the inner end of the buccal tube the cuticle is thickened to form two jaws laterally placed, each consisting of six transverse rows of teeth with about twenty in each row (Pl. IV, fig. 1, J); each tooth is secreted by a single epithelial cell. When the animal is feeding, the radula (R) works over the surface of the weed or other material to rasp off diatoms and algal cells, the jaws meanwhile gripping the substratum. The radula (Fig. 1 C) is made up of numerous

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EXPLANATION OF PLATE IV

Fig. 1.

Skeneopsis planorbis. Right lateral view of whole animal seen as a transparent object. × 80. A, anus; AH, anterior region of stomach; AL, anterior lobe of posterior pedal gland; AM, opening of anterior pedal gland; BU, buccal ganglion; C, columellar muscle; CD, ciliated duct leading from vas deferens to mantle cavity; CE, cerebral ganglion; D, duct of posterior pedal gland; DI, digestive gland; DP, penial duct; E, eye; EX, spherules in excretory cells of digestive gland; F, gill filament; GA, parapedal ganglion; GD, mucous glands opening on sole of foot; H, heart; I, intestine; J, jaw; K, kidney; L, opening of digestive gland into stomach; LI, left salivary gland; MA, mantle; MG, anterior pedal gland; OE, oesophagus; OL, opercular lobe of foot; OP, operculum; P, prostate; PE, penis; PG, pedal ganglion; PH, posterior region of stomach; PL, posterior lobe of posterior pedal gland; PR, pleural ganglion; R, radula; RA, radular sac; RI, right salivary gland; ST, snout; T, tentacle; TE, testis; TO, statocyst; V, vesicula seminalis.

Fig. 2.

Omalogyra atomus. Right lateral view of whole animal seen as a transparent object. × 120. AB, albumen gland; AG, anterior lobe of digestive gland; B, buccal cavity; BC, bursa copulatrix; CG, capsule gland; DA, duct of albumen gland; FC, fertilization chamber; GA, genital aperture; HD, hermaphrodite duct; HL, head lobe; KM, large glands opening into mantle cavity near anus; MG, anterior pedal gland; MU, mucous gland; MT, muscular tube; O, ovarian duct; OD, muscles of odontophore; OM, opening of albumen gland into mucous gland; OPE, opening of sperm sac into prostate; OV, egg in ovary; PD, pallial vas deferens; PM, opening of posterior pedal gland; PO, pallial oviduct; SP, sperm sac; ST, stomach. Other letters as in fig. 1 above.

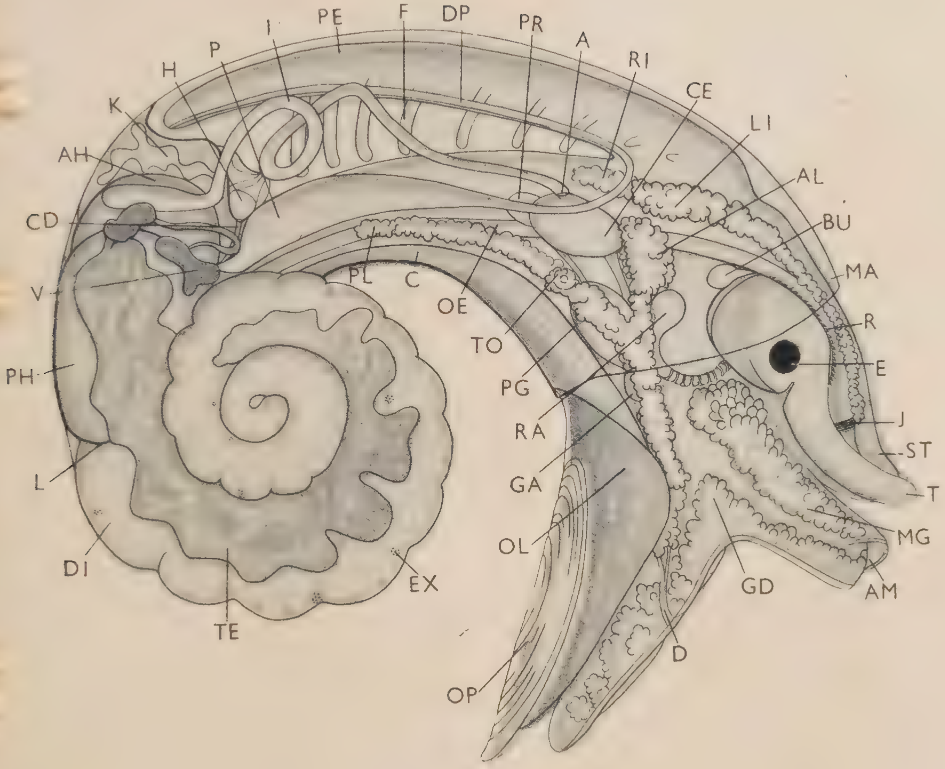
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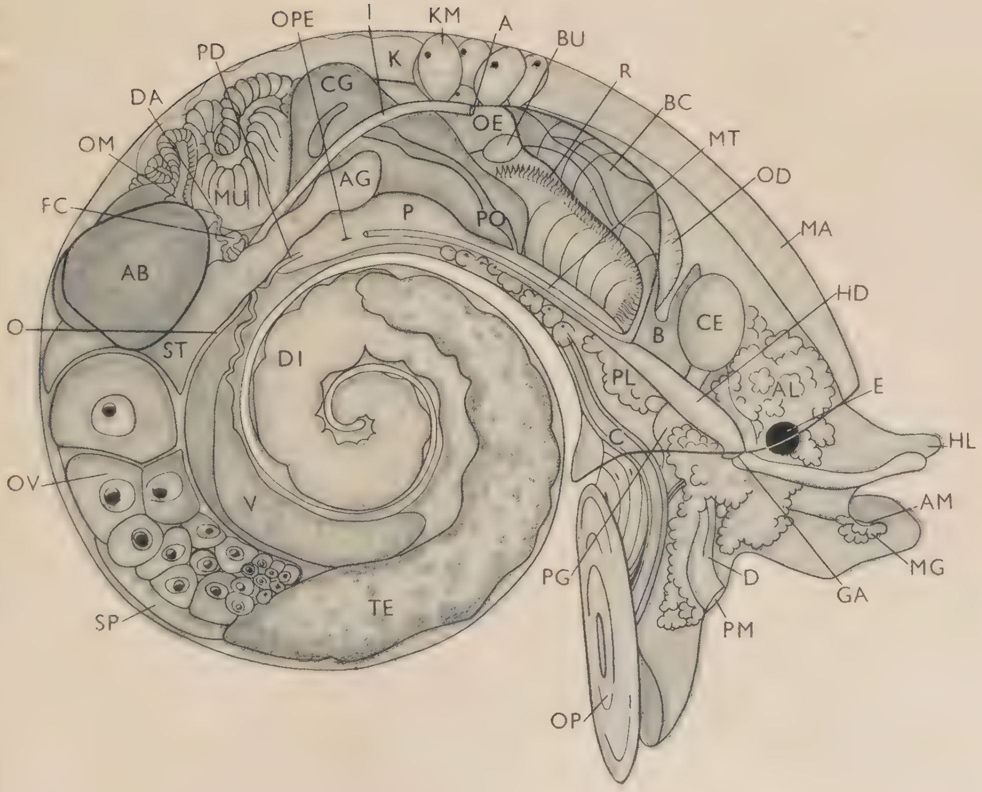
Fig. 1.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[illegible] very dilatable tube, a ventral [illegible] bears a cuticle, and this also spreads on [illegible] which the odontophore lies. At [illegible] the cuticle is thickened to form two jaws [illegible] rows of teeth with about [illegible] is secreted by a single epithelial [illegible] works over the surface of the [illegible] algal cells, the jaws meanwhile [illegible] the substratum. The radula (Fig. 1 C) is made up of numerous

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EXPLANATION OF PLATE IV

[illegible] lateral view [illegible] seen as a transparent object. ×80. A, anus; AH, anterior [illegible] lobe of posterior pedal gland; AM, opening of anterior pedal gland; [illegible] columellar muscle; CD, ciliated duct leading from vas [illegible] cerebral ganglion; D, duct of posterior pedal gland; DI, digestive gland; [illegible] spherules in excretory cells of digestive gland; [illegible] ganglion; GD, mucous glands opening [illegible] heart; I, intestine; [illegible] opening of digestive gland into [illegible] salivary gland; MA, [illegible] anterior pedal gland; OE, oesophagus; [illegible] of foot; OP, operculum; [illegible] PE, penis; PG, pedal ganglion; [illegible] region of stomach; PL, posterior [illegible] posterior pedal gland; PR, pleural [illegible] radular sac; [illegible] salivary gland; SN, snout; T, tentacle; [illegible] vesicula seminalis.

Fig. [illegible]

[illegible] lateral view of whole animal seen as a transparent object. ×120. [illegible] anterior lobe of digestive gland; B, buccal cavity; BC, bursa [illegible] DA, duct of albumen gland; FC, fertilization chamber; [illegible] hermaphrodite duct; HO, head lobe; KM, large glands opening [illegible] anterior pedal gland; [illegible] mucous gland; MT, muscular [illegible] muscles of odontophore; OA, opening of albumen gland into [illegible] sperm sac into [illegible] OV, egg in ovary; PD, pallial vas [illegible] pedal gland; PO, pallial oviduct; SP, sperm sac; ST, [illegible] above.

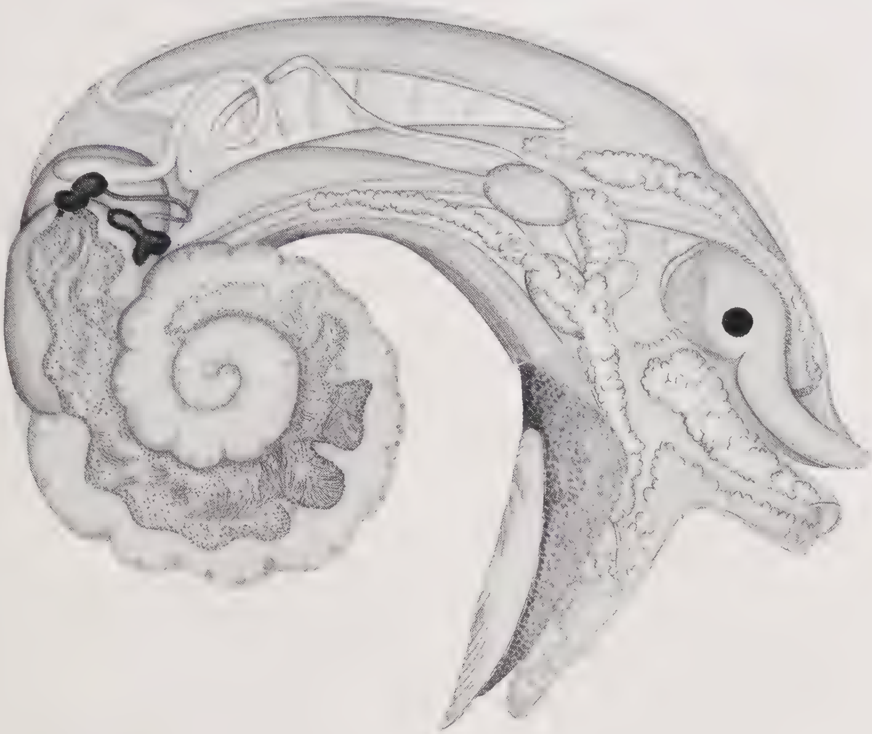
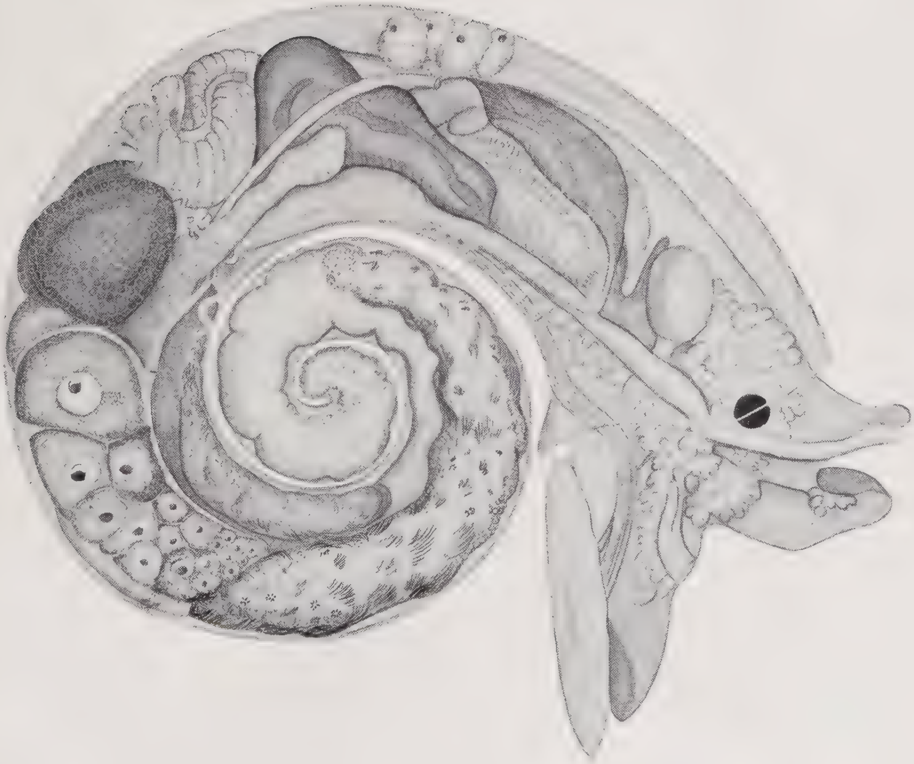


Fig. 1.



transverse rows of sharply cusped teeth, each row comprising a large central tooth (CT) bordered on each side by one lateral (L) and two marginals (G).

Along the mid-dorsal wall of the buccal cavity is a deep ciliated channel along which the food is directed to the oesophagus. The salivary glands (Pl. IV, fig. 1, RI and LI) open at the extreme anterior end of this channel, one on either side. Their secretion lubricates the action of the radula and entangles the food particles which are drawn in by it. The glands run parallel with the oesophagus as far as the nerve ring, the one on the left side being slightly longer than that on the right. Mucous cells provide the greater part of the saliva. There is, however, a second type of secreting cell filled with protein spherules which swell and dissolve when expelled, probably liberating an enzyme.

The oesophagus (OE) is a straight, narrow, ciliated tube of about the same diameter throughout. From its origin at the posterior end of the buccal cavity it is directed ventrally and slightly to the left of the median line, and traverses the length of the body whorl. There are no glandular pouches along its course, as are common amongst herbivorous prosobranchs, and the only secreting cells are epithelial mucous glands.

The stomach is spacious and lies at the posterior end of the body whorl, at right angles to which it is elongated. It is divided by a transverse constriction into two regions: an anterior (AH), which is dome-shaped and lined by a columnar ciliated epithelium, the cilia being thick and closely set; and a more posterior one (PH), the wall of which is, in the main, cuticularized. The upper, anterior, chamber corresponds to the style sac of style-bearing prosobranchs and the lower, posterior, chamber to the part containing the gastric shield. The anterior wall of the posterior chamber is ciliated where it receives the opening of the oesophagus at the level of the transverse constriction. At the extreme posterior end is the opening of the single lobe of the digestive gland (L). The stomach, especially its anterior compartment, is conspicuous in the living animal since there is a heavy deposit of black spherules in the epithelial cells. The intestine (I) arises from the dorsal wall of the anterior chamber and bends abruptly to pass forward on the right side. For a short distance along its initial length can be traced a longitudinal groove bordered by a fold of epithelium. This gutter, with its accompanying fold, arises on the wall of the duct from the digestive gland, passes forwards to the anterior chamber of the stomach and so reaches the intestine. It affords a path by which waste from the duct may be conveyed to the intestine.

On histological grounds the intestine may be divided into four regions. The initial part, in which the columnar ciliated cells are heavily pigmented with black spherules, and along which the channel from the digestive gland can be traced, passes to a slightly wider and more muscular tube in which mucous cells alternate with ciliated cells. Here the faecal pellets are moulded: the particulate waste from the stomach, which consists of diatom cases, algal cells and detritus, is agglutinated by means of mucus and compacted into oval rods.

These are still further elaborated in the third section of the intestine, the longest of the four, which takes a somewhat sinuous course as it accompanies the genital duct along the right wall of the mantle cavity. In this section the mucous cells are replaced by another type of gland which is scattered somewhat sparingly amongst the ciliated cells—it is conical in shape, with a broad base, and tapering distally, and towards the base is a large round nucleus, with a prominent nucleolus. The cytoplasm is dense and contains small secretion spherules which swell in the lumen of the gut and presumably help to harden the outer rind of the pellet. In the terminal or rectal region the cilia are longer than elsewhere and mucous cells are scattered in the epithelium, increasing in number towards the anus.

The digestive gland (DI), together with the gonad (TE), constitute the visceral mass which occupies the smaller coils of the shell. The gonad, frequently the smaller of the two glands, lies on the right side. The digestive gland has a segmented appearance, since it is made up of a series of lobes which open into one another and increase in size towards the stomach, into which they ultimately open. The epithelium of the gland consists of three types of cells: the most frequent, the digestive cell, is narrow at the base and gradually broadens towards a rounded distal end where there is a dense layer of protoplasm containing innumerable small spherules. These have been seen to be discharged and are probably enzymatic. The rest of the cytoplasm, except around the nucleus, is filled with vacuoles which vary in size, and contain during life either a clear refringent liquid or agglomerations of fine particulate matter sometimes embedded in a mucoid substance. No diatoms, algal cells or any such particulate food has ever been found within the lumen of the digestive tubules. The stomach, however, may often be seen filled with such objects, and since only empty cases of diatoms and the walls of broken cells are to be found in the intestine, it may be assumed that the bulk of the digestive process occurs in the stomach and that only the resulting solution, with perhaps minute particles, enters the liver, and is taken up by the digestive cells for further treatment.

The two other types of cell, neither of which attains the height of that already described, occur in the crypts of the tubules. In one, which appears to be excretory in function, the protoplasm may be highly vacuolated and an irregular clump of brown or black granules be contained in each vacuole. A more frequent appearance is when the cell contains only one large vacuole filled with a single spherical mass of such granules. These can be seen through the shell of a living animal (EX). They have never been found in the lumen of the gland. Somewhat similar cells of undoubted excretory function are described in the digestive gland of tectibranchs (Fretter, 1939), and it is probable that, as in that group, waste matter is absorbed from the blood through the broad bases of the cells. This, however, has not been tested owing to the difficulty of injecting such small molluscs.

The third type of cell may be grouped in small numbers around the excretory cell, though sometimes it occurs alone in larger numbers. In longitudinal section it is triangular in outline with a broad base resting on the basement membrane and a tapering distal end which hardly reaches the surface of the epithelium. The spherical nucleus lies towards the base and has a large nucleolus. The protoplasm stains deeply with iron haematoxylin and is vacuolated. Each vacuole contains a colourless refringent spherule which gives a positive reaction for lime. The probable function of these cells is either to act as a storage of lime for shell formation, or for the purpose of controlling the reaction of the secretion from the digestive gland.

The Reproductive System

The male. The testis (Pl. IV, fig. 1, TE), situated on the right side of the visceral mass, consists of a linear series of lobes which open broadly into one another and lead finally to the gonadial duct. This acts as a vesicula seminalis (V) which is dilated with sperm from the onset of sexual maturity. It coils on the right side of the stomach and then leads into a short narrow tube with a straight course, conducting the sperm from the vesicula seminalis to the prostate (P). This tube, the renal vas deferens, is surrounded by a layer of circular muscles which closes the lumen except when spermatozoa are actually passing through it during copulation. It opens into the prostate gland on a small papilla. Alongside this is a ciliated duct (CD) which leaves the prostate and runs dorsally to open into the mantle cavity. Such an outlet to the mantle cavity has been described in certain Stenoglossa and in *Lamellaria*, and provides an escape for unwanted sperm (Fretter, 1941).

For the rest of its course the male duct runs straight along the right side of the mantle cavity to the penis (PE)—this section comprises the pallial vas deferens and along the posterior half the epithelium is tall and glandular and constitutes the prostate (P). The gland cells, which rest upon a basement membrane, are broad at the base and each tapers slightly towards the distal end. Wedged between the distal ends are ciliated cells which drive the prostatic secretion forward along the duct. The prostate is surrounded by a thin layer of connective tissue in which both circular and longitudinal muscle fibres occur. Anteriorly it ends abruptly, the duct narrows and is lined only by a ciliated columnar epithelium. The musculature, however, is greatly increased, for the circular muscle forms a layer which in thickness exceeds twice the height of the epithelial cells. Here, and along the penial duct, the histology of which is similar, the spermatozoa are conducted by peristaltic action.

The penis is somewhat compressed laterally and tapers to a point, the duct through it (DP) running near its ventral surface to open at the tip. Externally it is covered by a slightly cuticularized epithelium, except along the narrow dorsal and ventral walls where longitudinal strips of epithelial mucous glands occur, the secretion from which assists the passage of the penis through the pallial groove of the female to reach the opening of the receptaculum seminis (Fig. 2, RE). Beneath the epithelium is a layer of circular and longitudinal muscle fibres, and through the thickness of the organ oblique and dorso-ventral fibres separate numerous blood spaces. These, when gorged with blood during copulation, so enlarge the penis that if the copulating partners be separated it is only after some minutes that the penis can regain its position of rest along the length of the mantle cavity.

The female. The ovary, on the right side of the visceral mass, occupies a position similar to that of the testis and extends as far as the posterior chamber of the stomach. From here a narrow ovarian duct (Fig. 2, O) passes towards the posterior end of the mantle cavity where it opens into the fertilization chamber (FC), placed at the posterior end of the pallial oviduct, and receiving a duct from the receptaculum seminis (DR), and another from the albumen gland (DA). Its walls are ciliated and muscular.

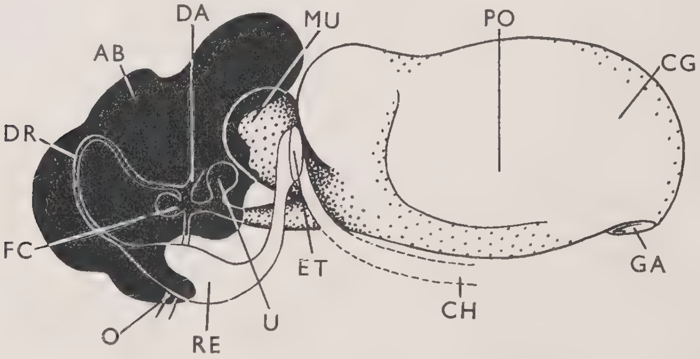


Fig. 2. *Skeneopsis planorbis.* Diagrammatic reconstruction of female genital duct. × 100. AB, albumen gland; CG, capsule gland; CH, channel along outer surface of mantle; DA, duct of albumen gland; DR, duct from receptaculum seminis; ET, entrance to receptaculum seminis; FC, fertilization chamber; GA, genital aperture; MU, mucous gland; O, ovarian duct; PO, lateral pouch of capsule gland; RE, receptaculum seminis; U, muscular sac.

The albumen gland is of considerable size (AB), and completely surrounds the fertilization chamber and the various ducts leading to it. The walls are thrown into a few deep folds, so that the gland has a lobed appearance, and they are lined throughout by a single type of cell in which the cytoplasm, except towards the base, takes up stains specific for mucus and contains somewhat large and irregularly shaped secretion masses of a protein nature, presumably albumen.

The oviduct extends along the right side of the mantle cavity. At first it is narrow and lined by ciliated cells, and, a short distance from the fertilization chamber, a muscular sac (U) opens into its dorsal wall. This sac is in the usual position for a receptaculum seminis, and might be its homologue, but it no longer functions as such and its use is unknown. The only point of interest concerning it is the enormous length of the cilia on the walls—at least five times the height of the cells. The pallial oviduct then thickens, and, for the rest of its course, except for a narrow strip along the ventral wall, the plan of the epithelium is essentially the same: gland cells alternating with ciliated cells. The initial part of this glandular section is narrow and both mucous and mucoid cells occur. It then opens into the ventral wall of a mucous gland (MU) which produces the inner mucous layer of the wall of the egg capsule, and here the lumen is elongated dorso-ventrally, the lateral walls being thick and the dorsal and ventral ones moderately thin. The ventral is composed of a low ciliated epithelium with occasional mucous cells, and a similar thin ventral wall extends as far as the genital aperture; it corresponds to the ventral channel of the pallial oviduct of other prosobranchs. Anteriorly, the mucous gland leads into the final and largest section of the pallial oviduct, the capsule gland (CG), where the egg capsule is retained whilst the main thickness of its wall is deposited. Here the lumen on each side is extended laterally to form a pouch of considerable dimensions (PO), though towards the genital aperture the duct gradually narrows. Three types of gland cells occur in the epithelium. Around the opening from the mucous gland there is a ring of cells in which the cytoplasm is filled with small protein spherules of uniform size. Mucous cells occur at the posterior limit of each lateral pouch and a considerable number lie around the genital aperture (GA). Elsewhere, that is, over the main area of the wall, the cytoplasm of the gland cells produces a fluid which has the appearance and consistency of conchiolin. Within the cells the secretion droplets stain lightly with iron haematoxylin and pale blue with azan.

Perhaps the most interesting point in the female genital system is the structure of the receptaculum seminis (RE). Between the pallial oviduct and the underlying columellar muscle the outer surface of the mantle—that is, directly under the inner surface of the shell—is folded to give a fairly deep longitudinal groove, the mouth of which faces outwards. The anterior end of the groove is about one-third of the length of the pallial duct behind the genital aperture. As it passes back the groove deepens and is subdivided longitudinally by a fold of epithelium to give an upper channel (CH) which leads to the receptaculum seminis, and a lower or ventral one which eventually narrows and disappears. The upper or dorsal channel is lined by tall columnar ciliated cells, the lower one by a squamous epithelium. The former passes postero-dorsally up the side of the mantle, and therefore parallel to and alongside the genital duct, and, meanwhile, twists through 90° so that it now lies more towards the dorsal side of the duct, the mouth of the groove pointing in that direction too. At the level of the middle of the mucous lobe of the pallial duct the lips of the groove fuse to form the entrance (ET) to a ciliated tube which leaves the surface of the body and passes deeper to enter the receptaculum seminis (RE). The receptaculum is an elongated pouch on the right of the genital duct and its posterior end is surrounded, except on the median side, by the albumen gland. Within it, the spermatozoa become orientated with their heads embedded in the epithelium. A narrow muscular duct (DR) leads from the posterior end of the receptaculum and takes a somewhat circuitous course to reach the fertilization chamber. The duct is surrounded by a thick layer of circular muscle, and only on rare occasions has sperm been seen in it. It would appear that during copulation the penis of the male is inserted between the shell and the mantle of the female on the right side, and directed along the course of the longitudinal groove. Its passage would be facilitated by the slight flattening of the penis and by the secretion from the mucous glands situated on its dorsal and ventral walls. The tip of the penis would then reach to the opening of the duct leading down to the receptaculum seminis. Sections of a female fixed immediately after copulation showed the receptaculum and the duct leading to it filled with spermatozoa. Such a specialized method of copulation is not known elsewhere in the Mollusca.

Reproduction and Life History

The egg capsule of *Skeneopsis* is described by Linke (1933). It is approximately spherical or ovate (0·45 mm. long, 0·35 mm. broad), though flattened along the surface by which it is attached to an algal filament. It contains one or two heavily yolked eggs which pass through a veliger stage within the capsule and hatch as miniatures of the adult. Each egg is surrounded by a layer of albumen which gradually diminishes as development proceeds, and the young molluscs come to occupy most of the space within the capsule. The wall consists of two layers, a fairly thin mucous lining, and a much thicker fibrous coat. The former is secreted by the posterior mucous lobe of the capsule gland, the latter by the anterior larger section of the pallial duct. Linke (1933) states that the full development takes from 3 to 4 weeks in sea water at a temperature of 12–15° C. At a slightly higher temperature (approximately 14·5–17·5° C.) eggs which were laid on weed in a finger bowl developed in 2½ weeks. The young rasp their way through the wall of the capsule by means of the radula.

Lebour (1937) states that *Skeneopsis planorbis* breeds throughout the year at Plymouth. This statement, however, requires amplification. From an examination of animals in rock pools around Cawsand, Plymouth, it is found that the majority are spawning during spring. These adult individuals measure at their broadest diameter 1·55 mm. on the average, which is also about the maximum size to which they grow in this locality. By the first week in June innumerable young are present, exceeding, in most rock pools, the number of adults, and the average breadth of these is 0·48 mm. Egg laying continues throughout the summer months, though by September it is decreasing and only a few animals are spawning as late as the end of October. By the new year the typical individual found in the rock pools has a diameter of 0·85 mm. and is sexually immature. A few perhaps exceed a millimetre. The older generation has by this time died out—only one or two individuals have ever been found—

so that it is in the main an immature population which tides over the winter, a population produced by the late spawners.

It would thus appear that *Skeneopsis* is an 'annual' with a normal breeding season during the spring or summer. This, however, may be extended in two directions: (1) to the earlier months of the year if the weather be suitable, by precocious ripening of the snails which have survived from the previous year; or (2) it may be prolonged into late autumn, again if the weather is kind, by the arrival at maturity of young which were hatched during the summer months and which would otherwise have to wait for the coming of the next spring.

OMALOGYRA ATOMUS (PHILIPPI)

Omalogyra is one of the most minute of British molluscs, as is suggested by its specific name. The shell (Fig. 3), which resembles that of a miniature *Planorbis*, measures only about 1 mm. at its broadest diameter. It is reddish brown in colour, coiled in a plane spiral, and, since the umbilicus is widely open, the interior of the spire is exposed. The shell is thus concave on both sides and has a bilateral symmetry about the sagittal plane. There are three whorls, compactly coiled, with the outer one, the largest, enwrapping the others which are exceedingly small and diminish in size towards the apex. Each is rounded on the outside, but somewhat flattened on the inside; the sutures are strongly impressed and deep. The mouth, approximately circular in outline, projects slightly outwards and has a sharp and even edge. The surface of the shell is glossy and smooth except for fine striae marking the lines of growth. The operculum (Pl. IV, fig. 2, and Fig. 3, OP) is white, circular and flat, with a slightly thickened spiral line which coils outwards from the centre to give three or four turns of increasing diameter.

The body is a uniform yellowish white, though little is exposed as the animal creeps along; the shell is then held erect with the mouth parallel to the substratum. The mollusc has a steady gait and the shell is rarely tossed to and fro as in *Skeneopsis*. Projecting anteriorly from the mouth of the shell is the broad, flat, flexible snout which is notched medially so as to form on each side a flat semicircular lobe (HL); the two lobes are joined by a straight and thin intermediate membrane beneath which is the mouth. Around the outer edge of each lobe and along the intermediate membrane is a row of stiff cilia which are presumably sensory in function: when the animal moves about it frequently waves the lobes in the water or presses them against the weed or rock as though sensing its environment. The lateral and posterior margin of each lobe is thickly ciliated. On the upper surface towards the posterior extremity is the eye (Pl. IV, fig. 2, E), which is large for the size of the snail; it is only just exposed when the animal creeps. No tentacles are present; functionally they are replaced by the lateral head lobes.

The foot, with sides approximately parallel, is rounded or slightly bilobed in front and rounded posteriorly. It is short in proportion to the length of the shell, beyond the posterior end of which it does not project, and rarely is it seen to protrude beyond the snout anteriorly. Its epithelium is thickly ciliated except for a cuticularized band at the junction of the foot with the body. Projecting from this cuticular surface, immediately beneath the head lobe on each side, and on a level with the eye, is a small tuft of tall ciliated cells. Fibres from the pedal nerves pass to them, and they may therefore be epipodial sense organs. There are two pedal glands. The anterior one (MG) opens on the upper surface of the propodium, where, directly in front of the mouth, there is a median ciliated depression (AM). The gland consists of unicellular mucous cells which are embedded in the substance of the foot beneath this depression and open singly between the ciliated cells. The posterior gland, which is much more extensive, has a longitudinal slit-like opening at about a third of the pedal length from the posterior end of the foot (PM). The ciliated duct (D), which passes dorsally from the opening, soon bifurcates into left and right branches and each of these, as in *Skeneopsis*, drains the secretion from two main glandular masses: one lies in front of the nerve ring and extends forwards between the eyes (AL), whilst the other (PL), lateral and more posterior, runs back beneath the genital duct on the right side, and, on the left, extends up the side of the odontophore. The posterior part of the gland is composed entirely of mucous cells, except for a few large cells at its extreme posterior end. These are filled with spherules which are readily dissolved on fixation leaving an inconsiderable amount of vacuolated cytoplasm. In the anterior part of the gland a different type of secreting cell accompanies the mucous cell, with spherules staining lightly with iron haematoxylin and deep red with azan. All the cells of the posterior pedal gland are arranged in groups, and each group has its own individual duct which leads to one main branch of the collecting duct. The gland is a useful possession for animals inhabiting rock pools; for *Omalogyra* often creeps on the surface film of water and can employ a thread of secretion to lower itself gradually into the water should it be disturbed, in exactly the same way as *Skeneopsis*. Also, when the mollusc is creeping over weed, or occasionally over rocks, its path is lubricated by the viscid secretion, and this gives the firm anchorage which is so necessary on a wave-washed shore, and which in the larger rock-clinging gastropods may be given by the more muscular type of foot.

The mantle cavity extends to the posterior end of the body whorl. Anteriorly, for a short distance, it completely surrounds the body, as the left and right lobes of the mantle fuse with one another beneath the columellar muscle. Farther back, near the anterior end of the odontophore, and between this and the anus (A), it is restricted mainly to the right side, but also extends over the dorsal surface of the body. On the left, where in other prosobranchs the ctenidium hangs down from the roof of the cavity, the body wall is fused with the overlying mantle: in *Omalogyra* there is neither ctenidium nor osphradium. Posterior to the anus the presence of the genital ducts, and of the kidney, confines the mantle cavity to the left of the median line so that it comes to overlie the oesophagus. The anus opens far back on the right side, a position which is probably secondary. From it, two longitudinal strips of ciliated columnar cells, extensions of the rectal epithelium, pass forwards to the mouth of the mantle cavity (omitted, for simplicity, from Pl. IV, fig. 2). The dorsal strip, which is the longer, runs along the roof to its edge, the ventral one along the body wall, ending on a level with the nerve ring. This appears to constitute a tract along which faecal matter is led to the mouth of the mantle cavity. In a living animal faecal matter can be seen through the transparent shell to leave the anus and to be directed forwards in this way, apparently rotating on its route. Below each strip lie mucous glands which discharge into the mantle cavity, some between the ciliated cells. The dorsal layer of glands is broader than the ventral and extends towards the median line; it represents the hypobranchial gland. At its posterior limit, in the vicinity of the anus, the mucous cells are replaced by a group of about a dozen enormous cells of another type, the openings of which lie close together (KM). It is these large glands which have been mistaken for eggs by Jeffreys (1867) and Lebour (1937). Each is broadly elliptical in longitudinal section, with the nucleus, near the base, surrounded by a dense layer of cytoplasm. Elsewhere the cytoplasm is vacuolated. There may be one vacuole which fills the greater part of the cell or several smaller ones; in living material each contains a colourless fluid. The secretion of these glands appears to be concerned as much in the elaboration of faecal pellets as in lubrication, and thus compensates for the absence of glands in the intestine. The pellets are rod-shaped, often with rounded ends, and are not so compacted as in *Skeneopsis*.

The kidney (K), which lies in the mantle, extends back from the level of the anus to the heart, which is directed obliquely across its posterior wall, with the auricle in front of the ventricle. The kidney is a simple vesicle in which the epithelium is not folded, as is typical of other molluscs, to increase the excretory area. Along its left wall runs the main pallial vein which branches anteriorly over the mantle and leads posteriorly to the auricle. The inner wall of the mantle is covered for the most part by squamous epithelium which separates the blood vessels from the flow of water in the underlying cavity. This water current is presumably set up by the cilia on the longitudinal strips of epithelium passing forwards from the anus, which are constantly beating towards the mouth of the mantle cavity. The gaseous exchange which occurs through the wall of the mantle is apparently adequate for the respiratory needs of a gastropod of such small size, and so explains the absence of any specialized respiratory organ.

The Alimentary Canal

The lateral walls of the extreme anterior end of the buccal cavity are thickened by an epithelium of considerable height bearing a cuticle. These thickenings act as jaws which grasp the weed as the radula plays over its surface. The odontophore is far removed from the mouth owing to the elongation of the buccal cavity in an anterior direction to form a proboscis-like tube. This tube is very distensible and is also cuticularized. *Omalogyra* is a pendulum feeder (Ankel, 1938) with *Ulva* as its favourite food: as it creeps slowly over the surface of a thallus the head is swayed to and fro whilst the surface cells of the alga are rasped by the radular teeth. The animal thus leaves behind it a zig-zag feeding trail (Fig. 3, FT). During the spring, summer and autumn months the stomach, and especially the cells of the digestive gland, are coloured green with chlorophyll from the weed. The contents of the plant cells which are rasped by the radula, and perhaps some severed pieces of alga, are mixed with mucus from the anterior pedal gland, sucked up into the buccal cavity and passed along the dorsal ciliated channel which lies above the odontophore. At the extreme posterior end of this channel the salivary ducts open, one on each side; they are extremely narrow tubes and each passes back to a compact group of a few large secretory cells. The dorsal channel leads imperceptibly into the oesophagus (Pl. IV, fig. 2 OE) which is about the same diameter throughout its length. In animals which are collected during the summer, when food is plentiful, the oesophagus is broader than in the winter and spring. Moreover, there is a histological difference between them: in *Omalogyra* which live through the winter the oesophagus is ciliated at its extreme anterior end, along the whole length of its dorsal wall and for a narrow longitudinal strip along the mid-ventral wall. Laterally, however, in a region comparable to the oesophageal pouches of other prosobranchs, it is lined by digestive epithelium which is identical with the digestive cells of the liver, and also comprises the lining of the stomach. In animals which develop and breed during the summer, the longitudinal glandular tracts of the oesophagus are not present, though the stomach has the lining of digestive cells, reminiscent of the embryonic condition of gastropods in which the liver cells cover the wall of the stomach only to be constricted off at a later stage. In these forms, too, the salivary

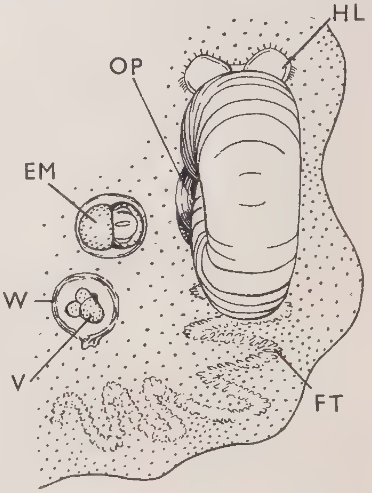


Fig. 3. *Omalogyra atomus*. Living animal feeding on *Ulva*. Two egg capsules are attached to the weed. ×45. EM, embryo at time of hatching; FT, feeding trail; HL, head lobe; OP, operculum; V, veliger; W, wall of egg capsule.

glands are relatively larger. The unusual distribution of the digestive epithelium in the adult is correlated with the type of food: the principal, perhaps exclusive, food is plant sap, and since this needs no mechanical treatment prior to digestion, the stomach is no longer necessary for this and can act as an extension of the digestive gland. Presumably in winter, when food is most scarce and when the animals are immature and undergoing slow development, the spreading of the digestive epithelium along the oesophagus enables a more thorough absorption of any food which may be obtained, or if the cells are capable of secreting enzymes it may permit a fuller utilization of the material. As the oesophagus passes back through the body whorl it is directed to the left and consequently gives ample space for the development of the voluminous genital glands on the right side; it opens at the extreme left of the antero-dorsal wall of the stomach. The stomach (ST), in proportion to the animal's size, is smaller than in *Skeneopsis*. The anterior wall not only receives the oesophagus, but the intestine (I) and anterior lobe of the digestive gland (AG) also open here. The intestinal aperture is median to that of the oesophagus, and a strip of ciliated epithelium, continuous with that of the oesophagus, runs across the stomach wall from oesophagus to intestine. The small anterior lobe of the digestive gland (AG) enters the stomach to the right of the intestinal opening. This lobe is not present in *Skeneopsis*, but only the much larger posterior one (DI), which leads from the posterior wall of the stomach and occupies the coils of the visceral mass. It would correspond with the left lobe of the digestive gland of other gastropods. This is always the larger of the two, since the right lobe—anterior in *Omalogyra*—is reduced as a result of torsion, and may be lost entirely. Each lobe in *Omalogyra* is a blind tube, constricted at regular intervals along its length, and the epithelium does not form the ramifications which are typical of the more solid construction of the liver of other gastropods. The digestive epithelium consists of two types of cells—digestive cells and rather infrequent lime cells. In the digestive cells the cytoplasm is vacuolated and the vacuoles seem to contain ingested food; no particulate matter has ever been found within them. The lime cells arise from a broad base and taper at the distal end; the cytoplasm is filled with large colourless spherules of calcareous matter.

The intestine is a short, straight tube which runs along the right side of the genital duct. Rather unusually there are no gland cells along its course. The cilia of the epithelium are so long that their tips meet across the tube and beneath the epithelium are a few circular and longitudinal muscle fibres embedded in a thin layer of connective tissue.

The Reproductive System

The gonad (Pl. IV, fig. 2, OV, TE) spreads over the surface of the digestive gland on the right side of the visceral mass. It is composed of two lobes lying alongside one another, one a testis and the other an ovary. In animals which have been collected in the spring and which have developed slowly from late summer or autumn eggs the genital system is in the male condition; the female organs are developed, but are not as yet functional. The anatomy of such an individual is shown in Pl. IV, fig. 2, and its reproductive system will now be described. The testicular duct (V) acts as a vesicula seminalis. It leads, by a somewhat sinuous course, to the posterior end of the body whorl, on approaching which it narrows and is surrounded by a sphincter. The duct opens into the fertilization chamber (FC), a muscular pouch lined by ciliated epithelium, and into this there also passes (i) the ovarian duct (O) which at this stage is retarded in its development, (ii) the duct of the albumen gland (DA) and (iii) the pallial vas deferens (PD). The pallial vas deferens passes along the right side of the mantle cavity and is initially narrow and ciliated. Soon, however, it broadens and is surrounded, except on its ventral side, by numerous gland cells. The outer ends of these pass between the circular muscle fibres beneath the epithelium and form a thick subepithelial layer. In sections stained with iron haematoxylin and counterstained with mucicarmine, the differences between the epithelial and subepithelial parts of the cell are most pronounced. In the latter the cytoplasm stains rather deeply with iron haematoxylin, and spherules in the cytoplasm may be either a very pale grey, and slightly affected with mucicarmine, or a few small ones may be stained black. In the distal region the cytoplasm stains pink and the spherules may be either a deep pink or black. The latter occur towards the free tips of the cells and probably represent the final stage in the elaboration of the secretion. These glands constitute the prostate (P) and surround the pallial duct for about a third of its course.

Normally, in the mesogastropods, the pallial vas deferens leads to a penis which lies on the right side of the head, a muscular organ which is distended with blood during copulation. *Omalogyra*, however, has no such penis, and its method of copulation would appear to be unique amongst the molluscs.

Lying in the lumen of the prostate, and projecting back from an anterior origin, is a muscular tube (MT) which is open at its distal end to the prostatic cavity. Around the opening the walls are ciliated. Elsewhere, inside and out, the epithelium of the tube is covered by a thin cuticle; beneath the outer epithelium is a layer of circular muscles, and a layer of longitudinal muscles underlies the inner epithelium. The tube passes forwards beyond the anterior limit of the prostate, where the genital duct narrows, and it comes to occupy the greater part of the lumen of this part of the duct. Here the epithelium of the genital duct is also cuticularized and surrounded by circular muscles of considerable thickness. At some distance from the genital aperture the tube originates from the wall of the vas deferens. Closer investigation of this region shows that it actually passes through the dorsal wall of the duct, and enlarges into a muscular sac (BC) which lies in the haemocoel, and spreads over the right wall of the odontophore on to its dorsal surface. It is as though the lips of the opening of this sac had been pulled out to form a long tube which lies in the duct to which the pouch connects, pointing towards the visceral mass. The histology of the sac is similar to that of the tube except that it lacks an outer epithelium. It is homologous with the bursa copulatrix of other forms. Strictly, the origin of the bursa is from an hermaphrodite duct (HD), since posterior to that point the pallial oviduct (PO) joins the vas deferens by way of an extremely minute opening surrounded by a sphincter. But obviously at this stage the oviduct is not functional and the main channel is, in effect, a male one. The hermaphrodite duct, which is extremely muscular, appears as a forward continuation of the vas deferens and opens anteriorly on the right side of the head (GA), just within the shelter of the mantle. It is lined by a slightly cuticularized epithelium in which there are a few mucous glands.

One other structure which is associated with the male genital system and which, like the elongated neck of the bursa, is only present in animals collected during the spring months, has yet to be described. It is a sac which lies against the left wall of the ovary (SP), and is connected to the posterior end of the prostate (OPE) by a narrow ciliated duct. The duct passes antero-dorsally on the left side of the stomach, and over the posterior end of the oesophagus to reach the thickly ciliated ventral wall of the prostate. The sac, which will be referred to as the sperm sac, is lined by an epithelium in which the protoplasm is highly vacuolated, and the nuclei are large with prominent nucleoli. In fixed material many vacuoles appear to contain a loose coagulum, and in the living state a somewhat watery fluid. The sac, and sometimes also the duct, may be distended with sperm and a mucoid secretion, presumably derived from the prostate.

The suggested mode of functioning of these male reproductive ducts is as follows. Animals collected in spring show the vas deferens as the principal pallial genital duct, and at this stage the opening of the pallial oviduct into the hermaphrodite duct is far too small to allow the passage of an egg capsule—in other words, the animal is purely male. Since the tube which extends from the opening of the bursa is an extremely muscular organ, and blocks the passage through the anterior end of the vas deferens, and since the bursa itself is also at this time extremely distensible, it may be assumed that, with the absence of the normal type of penis, these structures are concerned in copulation. The only means by which this seems possible is for the tube to suck up, by peristaltic action, sperm liberated from the vesicula seminalis, and prostatic secretion. These would then fill the bursa. The direction of the penial tube might then be reversed and it could be protruded through the muscular hermaphrodite duct so as to project from the genital aperture and pass into the duct of the copulating partner. Into this the sperm from the bursa would then be passed by muscular action. However, during the male phase no contents have been found in the bursa or in the penis. I do not know what part of the genital system receives spermatozoa, and have been unable to discover whether there is a mutual cross-fertilization or not.

The function of the sperm sac, which, it will be recalled, is found in the male phase only, is probably to clear the pallial vas deferens of sperm and prostatic secretion which have failed to enter the copulatory organ. Sections suggest that here the spermatozoa undergo disintegration: they appear to be digested and the final products absorbed by the vacuolated epithelial cells.

For the investigation of the female genital system it is necessary to examine animals collected in the months June to September. The eggs (Pl. IV, fig. 2, OV) in the ovary are relatively enormous even before the female system is functional, and appear to be out of all proportion to the size of the ovarian duct (O) along which they pass to the fertilization chamber (FC). From there the eggs are carried to the albumen gland (AB), which is divided approximately into two lobes lying side by side and communicating with one another along their adjacent walls. The short ciliated duct (DA) from the fertilization chamber opens into the anterior end of the right lobe, whilst at the anterior end of the left a narrow though muscular passage (OM) leads into the mucous gland (MU). Along this route the eggs are conducted. The epithelium of the albumen gland is composed of a single type of secreting cell. The mucous gland is of a rather irregular shape owing to the folding of its walls; the epithelium is high and the gland cells alternate with ciliated cells which are wedged between their distal ends.

The capsule gland (CG) is the next and last section of the pallial duct, and receives the eggs from the mucous gland; it lies on the right side of the pallial vas deferens and not above it as in the male phase (Pl. IV, fig. 2). Its secreting cells have a mucoid cytoplasm which is vacuolated and in the vacuoles are irregularly shaped protein spherules. Wedge-shaped cells, which lie between the distal ends of the secretory cells, are covered with closely set short cilia. The basement membrane is surrounded by a layer of circular muscles which thickens at the entrance to the hermaphrodite duct.

In all animals which have been collected in June and the succeeding months of the summer, that is, during the height of the breeding season, the reproductive system in all stages of maturity shows certain fundamental differences from the male phase: no tube extends from the lips of the bursa and no sperm sac is present; the capsule gland, now more voluminous, lies on the right side of the vas deferens, and not above it, and is broadly open to the hermaphrodite duct anteriorly; the pallial vas deferens is glandular along its whole length and its junction with the left wall of the oviduct, to form the hermaphrodite duct, is by way of a minute aperture surrounded by a sphincter. Certain changes have occurred in the structure of the bursa. It now opens by way of a muscular ciliated duct which is of considerable length, so that the sac itself appears to occupy a more posterior position and often lies behind the odontophore, between the oesophagus on the left and the male duct on the right. Its musculature is insignificant—in fact it is only with difficulty that any muscle fibres can be seen at all—and its epithelium is no longer cuticularized. The cells are larger, with vacuolated protoplasm and the nuclei are spherical and have prominent nucleoli. The histology of the bursa in the female phase resembles that of the sperm sac in the male phase, and the function of these two structures appears to be similar, for within the bursa waste secretion from the genital ducts may accumulate and later be disposed of; the accumulation is greatest after an egg capsule has been deposited. On histological grounds the hermaphrodite duct may be divided into two distinct regions. The first is lined by a ciliated and glandular epithelium in which mucous cells alternate with ciliated cells, and there are a few subepithelial mucous glands. In the second, which leads to the genital aperture, the epithelium is low, cuticularized and thrown into slight longitudinal folds. Below it lies a thick coat of circular and longitudinal muscles, and a sphincter surrounds the genital opening.

Originally it was thought that every animal passed through a functional male phase with the genital structure as shown in Pl. IV, fig. 2, and later the reproductive system underwent certain changes associated with the adoption of the female phase—this would account for the differences noted above. This may indeed be true for the animals which survive the winter and are the early spring spawners. Although the transition has not been followed in any detail, some individuals collected in mid-April do show the capsule gland enlarging around the right wall of the vas deferens, and a reduction in the size of the sperm sac and of the penial tube. It is now known, however, that individuals which hatch from eggs of summer spawners fail to develop the full anatomical characteristics of the male, and pass directly into a state anatomically comparable with the completely feminized individual. This anatomical femaleness, however, does not prevent the formation of apparently ripe spermatozoa in the testis and their passage into such parts of the male system as are present, and although the lack of a penis and associated structures would appear inevitably to preclude copulation and cross-fertilization, it may not be incompatible with successful self-fertilization.

Reproduction and Life History

No description of the egg capsule of *Omalogyra* is known. Jeffreys (1867) states that capsules 'are occasionally found in the upper cavity of the last whorl in dried specimens', and Lebour (1937) regarded the large glands which open near the anus as egg capsules, and assumed, from the very young crawling stages she observed, that direct development occurred.

The capsules are laid during the spring, summer and early autumn. They are irregularly spherical or ovoid (Fig. 3), and only slightly flattened along the surface which anchors them to weed (*Ulva* and *Enteromorpha*). Each measures 0·2 mm. in diameter, or $0{\cdot}17 \times 0{\cdot}20$ mm., and contains one or occasionally two eggs surrounded by albumen and encased in a wall (w) which consists of two layers. The inner is a mucous layer, and the outer is thick, rather adhesive and of a composite texture which gives a fibrous appearance and a somewhat wrinkled surface.

The eggs are fertilized either in the fertilization chamber or in the albumen gland: in a ripe female spermatozoa have been found in both of these. From the albumen gland the egg and albuminous secretion pass into the mucous gland, and here the inner layer of the capsule wall is added. The outer wall is manufactured by the capsule gland, to which the egg and its coverings is next transferred, and where it is detained for a much longer period. On two occasions a capsule has been found here, distending the duct to apparently abnormal proportions. The capsule is finally fixed to the weed, on which the adults are living, by pressure applied by the foot.

The development of the egg was studied during the month of August when the temperature of the sea water was high (15·0–18·5° C. day temperatures). A typical veliger (V) occurs, though the young develop to the crawling stage (EM) before they emerge. At this stage the individual practically fills the entire space within the wall of the capsule, the albumen being apparently used as food, and often it may be seen moving around the confined space with difficulty. Pressure thus exerted against the wall, together with the action of the radula, may assist hatching. The development is very rapid and is completed in about 10 days at the above temperature. On hatching, the small active molluscs, which measure about 0·16 mm. in diameter, begin to feed on *Ulva* and *Enteromorpha*, and appear to feed continuously. Their growth rate is rapid. In a week the size is doubled, after 17 days the average length is about 0·55 mm., and by the end of 5½ weeks the reproductive organs appear to be functional.

Throughout the summer numbers of individuals of all sizes are abundant; during the autumn the numbers fall until in December and January it is frequently difficult to find more than half a dozen specimens in a rock pool which in summer contained hundreds. The specimens which have been collected during the winter months are immature, of an average length of 0·57 mm., and are apparently hatched from the eggs of late spawners; by March the average length of the individual is 0·77 mm. This would suggest that, as in *Skeneopsis*, animals which have bred do not survive the winter. There is no indication that they migrate elsewhere or choose another habitat. Thus immature individuals tide over the winter and their growth rate is exceedingly slow. In spring they attain maturity, copulation occurs, and egg capsules are produced. The rate of reproduction increases with the rise in temperature and prolific growth of weed in the early weeks of summer. From the anatomy of adult individuals in summer it would appear that self-fertilization may then be practised. Some indication of the rate of increase in numbers during August was obtained from sixty individuals which were kept in a finger bowl and supplied with *Ulva*: after 3 weeks 156 young were produced and there were 21 embryos.

RISSOELLA DIAPHANA (ALDER)

The two species of *Rissoella*, *R. diaphana* (Alder) and *R. opalina* (Jeffreys) occur in intertidal coralline pools, together with the two genera which have been described. Externally the species are readily distinguishable by the shape of the shell and by the tentacles and snout (Figs. 4 and 6), but on the whole their internal anatomy is similar.

The shell of *R. diaphana* has the appearance of a rather short oblique cone, whitish in colour, smooth except for the faint markings of the lines of growth (Fig. 4, LG). It is extremely thin and transparent so that the cream, brown and orange coloration of the underlying viscera are exposed to view. There are four and a half convex whorls separated by fine though well-defined sutures: the apical one is blunt and rounded, and they gradually enlarge towards the mouth, the last occupying three-fifths of the entire spire. The mouth of the shell is large with an outer lip which is incurved and somewhat expanded below. The inner lip is sinuate—it follows the curve of the pillar of the shell and is slightly reflected. The exposed parts of the body of *R. diaphana* are yellowish white with brown pigment patches occurring on the opercular lobes of the foot (OL), an isolated streak on each side of the foot anterior to these, and on the head, between the eyes, a narrow median longitudinal streak which expands anteriorly to the middle of the upper lip, and posteriorly along the neck. In some specimens the pigmentation is more intense, of a purple-brown colour, and covers all the exposed surfaces of the body. Through the transparent colourless shell, on the dorsal surface of the body whorl, wavy streaks of light brown pigment in the underlying mantle are conspicuous against a general background of deep cream. On the right a deep brown blotch, the outer pigmented covering of a group of glands, marks, approximately, the position of the anus. Through the coils of the spire may be seen the deep brown digestive gland, accompanied on the columellar side by the gonad, which is of an orange colour. The transparency of the shell is so great that even the different types of cells in the digestive gland can be distinguished: the excretory cells as black dots scattered throughout the gland, the lime cells with their colourless refringent spherules and, most frequently, the brown digestive cells.

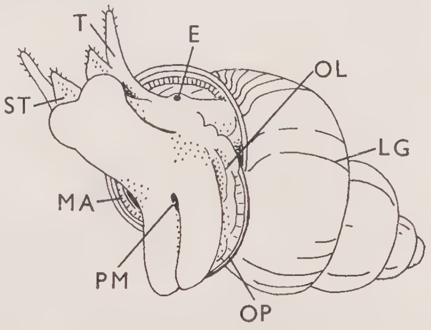


Fig. 4. *Rissoella diaphana*. Living animal. ×50. MA, mantle. Other letters as in Fig. 1.

The snout (ST) is bifid and forms two triangular lobes which diverge from one another at an angle of about 45°. These lobes are shorter and stouter than the tentacles (T) which arise one at the base of each, and the tentacles are cylindrical and taper slightly towards a blunt tip. Each is covered, at least around the distal half, by stiff cilia, and these also fringe the margins of the snout. The eyes (E) are small and placed on slight protuberances far back on the neck, so that when the animal is creeping they lie beneath the shell and never emerge from its shelter.

The foot is more or less lanceolate, somewhat bilobed in front and rounded or bluntly pointed behind; the opercular lobe on each side projects beyond the lateral margins of the sole, which is covered by short thick cilia. Between the ciliated cells open the ducts of subepithelial mucous and mucoid glands. The pedal mucous gland opens on a ciliated V-shaped depression on the upper surface of the foot just in front of the mouth, the angle of the V being directed posteriorly. At about half the pedal length from the anterior end of the sole is a median longitudinal slit, the opening of the posterior pedal gland (PM). This leads into a ciliated duct which, as in *Skeneopsis* and *Omalogyra*, bifurcates into left and right branches, each of which receives the openings of unicellular mucous glands. From the opening of the gland a temporary longitudinal groove, passing back to the posterior tip of the foot, may be observed in the living animal. Along this groove cilia direct the secretion which is an essential part of the locomotor mechanism of the animal.

The general layout of the organs associated with the mantle cavity of *Rissoella diaphana* resembles that of *Omalogyra atomus*. The cavity extends along the body whorl and contains neither gill nor osphradium. Posteriorly it is reduced in size by the massive pallial section of the female duct which projects dorsally from the body wall. The anus is far back on the right side, and from it the dorsal and ventral walls of the rectum are produced anteriorly towards the head as two longitudinal strips of columnar ciliated cells—one along the roof and the other along the floor of the mantle cavity. The former extends farther forwards than the latter. Below each is a broad band of secreting cells which open in, and on either side of, the ciliated strip; the dorsal band is the broader and is composed entirely of mucous cells. It represents the hypobranchial gland. The ventral one is composed of mucous and mucoid cells, the former opening on the median and the latter on the lateral side of the ciliated epithelium. Faecal matter—diatom cases, pieces of algal filaments and detritus—is directed forwards between these ciliated strips and agglutinated by the secretion from the adjacent glands. Broad, oval pellets are thus expelled from the mantle cavity. Near the anus, and on its median side, is a group of large gland cells, about six in number, which open into the mantle cavity. They are surrounded by a thin coat of connective tissue in which dark brown pigment granules occur, and they constitute the conspicuous blotch which is always seen through the transparent shell. In each cell the cytoplasm is filled with very large vacuoles which contain secretion spherules: these dissolve rapidly in acid fixatives. On the median side of the ventral longitudinal strip of gland cells is a deep gutter into which the female duct opens at the summit of a long papilla, and at the anterior end of which is placed the penis. The latter, when at rest, is folded back along the groove so that its tip lies immediately in front of the female aperture.

As in *Omalogyra* the kidney spreads forwards into the thickness of the mantle and opens near the anus. It is a simple sac lined by glandular tissue except for the dorsal wall where squamous cells occur. The glandular tissue is supplied by blood capillaries which are separated from the water current in the mantle cavity only by the squamous epithelium of the floor of the mantle. Through these capillaries the blood is filtered on its way to the efferent pallial vessel which passes along the left wall of the kidney.

Owing to the absence of a ctenidium, which is normally responsible for the setting up of a water current through the mantle cavity, *Rissoella* must depend upon other ciliated tracts for this purpose. Of these the longitudinal strips running forwards from the anus are the most powerful and maintain an exhalant stream. On the right side of the mantle is a band of columnar ciliated cells—a vestige, perhaps, of the ctenidium—where the direction of the effective beat of the cilia has not been determined, but together with a strip of similar epithelium on the underlying body wall they probably produce an inhalant current. Around the inhalant opening of the mantle cavity is a prominent tuft of ciliated cells which beat to the exterior and, as in other prosobranchs, they may expel the largest and heaviest particles which are drawn into the cavity with the stream of water.

The Alimentary Canal

The food of *R. diaphana* consists of diatoms, detritus and small algal filaments. These are collected by the radula whilst the object on which they occur may be held by the jaws. These comprise numerous teeth on the lateral walls of the buccal cavity, each secreted by a single cell and having a finely serrated edge. Anteriorly the buccal cavity is protected by a cuticle, and in the epithelium are a few mucous cells. The secretion from the anterior pedal gland, which opens immediately beneath the mouth, may assist in lubricating the action of the radula and agglutinating the small food particles. The radula is similar to that of *R. opalina* (Thiele, 1929) in that there is one central and two intermediate teeth, the lateral or marginals being absent.

The dorsal food channel, above the radula, conveys the food into the oesophagus. From its origin the oesophagus curves abruptly ventrally and to the left of the radula sac. Its displacement is due to the enormous growth of the reproductive ducts which fill the haemocoel dorsally; immediately behind the odontophore they cross to the right side to open into the mantle cavity. For the same reason the salivary glands, which open into the posterior end of the buccal cavity, are displaced; they are ventral in position, the left slightly anterior to the right. Each gland is a small tubular structure consisting of a comparatively few large cells which are of two types occurring in about equal numbers. There are mucoid cells and glands which, perhaps, produce an enzyme. The oesophagus is lined throughout its length by a ciliated epithelium. It passes beneath the albumen gland to open ventrally into the anterior wall of the stomach.

The stomach, approximately spherical in shape, lies at the posterior end of the body whorl. Dorsally, along its anterior wall, it receives the opening of the intestine, and ventrally the opening of the oesophagus. There are two liver ducts, one dorsal, well behind the origin of the intestine, the other ventral and posterior to the oesophageal opening. The epithelium lining the anterior half of the stomach is ciliated, but posteriorly is an extensive gastric shield. The stomach usually contains a large quantity of food, apparently mixed with fluid from the digestive gland, and compressed into a bolus by the cuticle of the gastric shield.

The two lobes of the digestive gland are unequal in size. That opening into the dorsal wall of the stomach is the smaller and spreads forwards to the posterior end of the albumen and capsule glands. It corresponds to the smaller right lobe of the gland of other prosobranchs. The second lobe, which opens ventrally, constitutes the greater part of the gland and spreads through the smaller coils of the visceral mass with the hermaphrodite gland. The digestive epithelium consists of three types of cells: one, which may be termed the digestive cell, arises from the basement membrane to a broad club-shaped distal end. The cytoplasm is vacuolated and in the upper half of the cell lie spherules which are probably enzymatic and are frequently seen in the digestive tubules. In the lower half of the cytoplasm are greenish brown masses, circular or irregular in outline, which may be absorbed food. No particulate matter has ever been seen in the tubules of the liver, only the same greenish brown fluid as occurs in the stomach. Another irregularly scattered type of cell of varying shape is excretory in function and contains spherules usually of a deep brown colour. Frequently their base is broad and the cytoplasm contains numerous small spherules, those near the base staining moderately intensely with iron haematoxylin, whilst the more distal ones are unaffected. At what appears to be a later stage in their development, these fuse to give a brown homogeneous mass. None of these masses has been traced in the faecal matter. It may be that, since the mollusc is an annual, waste matter, extracted from the blood, is rendered harmless within these cells and accumulates throughout its life. The third type of cell in the digestive gland is of large size and contains spherules of calcareous matter.

The intestine is a short tube which from its origin passes posteriorly for a short distance and then runs abruptly forwards along the right side of the genital duct to the anus. It is lined by columnar ciliated epithelium in which there appear to be no gland cells.

The Reproductive System

The gonad, which lies on the columellar side of the visceral mass, is a hermaphrodite gland with sperm and ova developed in the same tubules. A single and very distensible gonadial duct leads to the posterior end of the body whorl. Proximally it acts as a vesicula seminalis which contains sperm even when eggs are passing through it. Simultaneous hermaphroditism occurs, though, as is the usual rule, the male system is more precocious in its development than the female. The distal end of the gonadial duct (Fig. 5, HD) is lined by columnar ciliated epithelium, and on reaching the posterior end of the body whorl it divides into two branches which diverge from one another, one of these leading to the pallial vas deferens (PD) and the other to the albumen gland (AB).

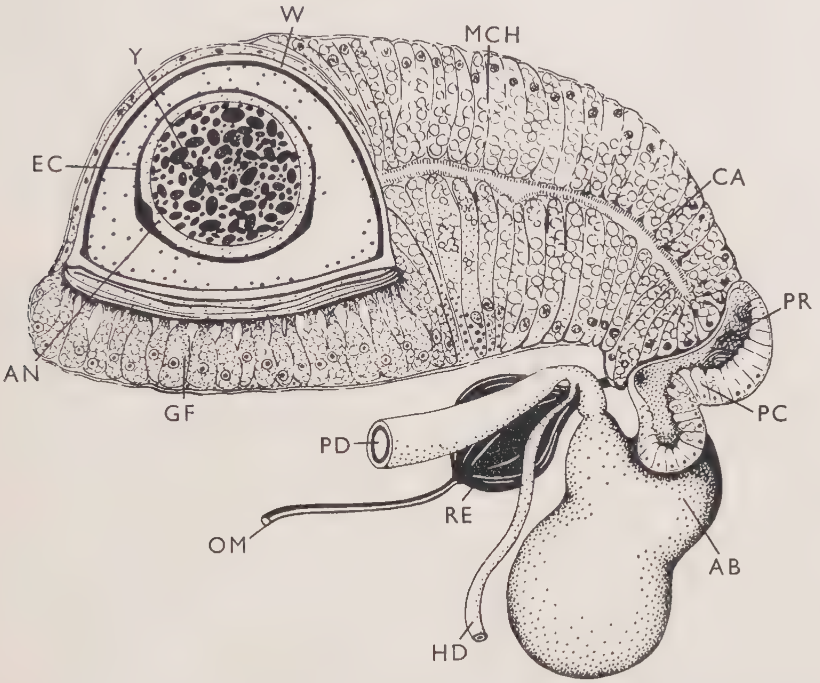


Fig. 5. *Rissoella diaphana.* Section through capsule gland and a reconstruction of the associated parts of the reproductive system. × 150. AB, albumen gland; AN, albumen; CA, gland cells producing a secretion similar to that of the albumen gland; EC, egg covering; GF, glands which thicken the floor of the egg capsule; HD, hermaphrodite duct; MCH, glands producing a mucoid-conchiolin fluid; OM, opening to mantle cavity; PC, posterior lobe of capsule gland; PD, pallial vas deferens; PR, spermatozoa; RE, modified receptaculum seminis; W, outer wall of egg capsule; Y, yolk granules of egg.

The vas deferens passes forward beneath the pallial oviduct, that is, on the left of the median line, and during this part of its course it is ciliated and a few circular muscles underlie the epithelium. Near the posterior end of the buccal mass the duct becomes glandular and turns at an obtuse angle across the dorsal surface of the body to the right side. It ends in a relatively short tubular penis, which, when at rest, lies folded back along the groove in the body wall. The glandular section of the duct constitutes the prostate. Here ciliated cells alternate with gland cells, one type of gland occurring posteriorly, and another along the anterior part of the duct. In the posterior glands the cytoplasm is vacuolated except towards the base where it is extremely dense. The vacuoles contain large spherules which have a composite structure; after the iron haematoxylin stain the general substance of the spherule is a rather yellowish grey, and embedded in it, or lying over its surface, are deeply staining bodies which may be kidney-shaped, comma-shaped or linear. The second type of gland, which covers a smaller area and extends to the base of the penis, contains small colourless and homogenous secretory spherules. No glands occur in the penis, and a ciliated columnar epithelium lines the tube.

The albumen gland is of considerable size, and is composed of a tall glandular ciliated epithelium of the usual type for this situation. It is probable that fertilization occurs within the gland, for during the breeding season spermatozoa are frequently found there. The gland opens into the posterior lobe of the capsule gland (PC), the ventral and anterior walls of which are thin and ciliated, and receive not only the duct of the albumen gland, but also the extremely narrow opening of a pouch which is presumably homologous with the receptaculum seminis (RE). It does not, however, function as such: it appears to receive unwanted secretion, such as albumen and excess shell material, and spermatozoa from the pallial oviduct. After an egg capsule has been laid the pouch is enlarged by enormous quantities of this material, whereas at other times it may be of quite minute dimensions. In addition to the connexion with the capsule gland a second narrow and thin-walled duct leads from the pouch to the mantle cavity (OM), and through this the surplus secretion and spermatozoa are passed to the exterior—there is no indication that the mollusc puts it to any profitable use. The glandular walls of the posterior lobe of the capsule gland (PC) produce a secretion of conchiolin-like consistency impregnated with mucus. Anteriorly the capsule gland leads forwards above the oesophagus and slightly to the right of the mid-dorsal line; it is a comparatively voluminous structure and projects from the dorsal body wall as an opaque white mass. It opens into the right side of the mantle cavity by way of a muscular papilla which is posterior to the root of the penis and well behind the tentacles.

Except in the region of the papilla, the walls of the capsule gland are thickened by tall epithelial secreting cells which alternate with wedge-shaped ciliated cells. In transverse section the lumen is approximately semilunar in shape, with the concavity directed ventro-medially. There are thus two longitudinal grooves along the duct: the outer or right one is the more pronounced, is thin-walled, not glandular, and folds beneath the glandular tissue of the floor. It originates along the wall of the genital papilla and passes back to the posterior lobe of the capsule gland, near the opening of the albumen gland. On several occasions spermatozoa have been found along its posterior end, not orientated, but scattered in irregular masses, and it would therefore seem to be the path along which these travel to the site of fertilization. On a histological as well as a functional basis the secreting part of the duct, anterior to the posterior lobe of the capsule gland, may be divided into three regions. In the most posterior of these the gland cells form a complete band around the duct, and are similar in many respects to those of the albumen gland, though they stain deeper with mucicarmine and purple with toluidin blue (CA). The succeeding glandular belt resembles the posterior lobe in producing a mucoid conchiolin fluid (MCH). The final glandular section comprises, dorsally and laterally, only a very narrow band of cells, though along the floor it thickens and spreads towards the genital papilla. The glands produce a basophil secretion which is added chiefly to the floor of the capsule (GF). The muscular papilla is separated from the glandular duct by a sphincter; it is lined by ciliated cells and a few mucous cells.

Reproduction and Life History

The egg capsules are manufactured one at a time in the pallial oviduct. They are described by Lebour (1936). Each is hemispherical in shape and attached by the flattened base to green or red algae, the base measuring 0·48 mm. long and about 0·25 mm. broad. The capsule contains one or two eggs (Fig. 5, Y), each covered by a thin membrane, albuminous layer (AN) and egg covering (EC), and floating in a fluid which fills the capsule. The outer wall (W) is thick and semi-transparent. During early summer several individuals of *R. diaphana*, with capsules still in the process of formation, have been fixed and sectioned (Fig. 5), and from these the functions of the various parts of the capsule gland have been calculated. The egg is presumably fertilized and receives its supply of albuminous fluid as it passes through the albumen gland (AB), and in the posterior lobe of the capsule gland (PC), where excess spermatozoa are frequently found (PR), the egg covering is deposited. The staining properties of this covering, which isolates each egg from its neighbour, and those of the glands of the posterior lobe are identical. The fluid which fills the capsule is derived from the next section of the duct (CA) as the egg passes forward, and the outer wall (W) from the two ultimate glandular regions. The more posterior of these forms a substantial layer of conchiolin impregnated with mucus (MCH), and this is covered, especially along the base of the capsule, by secretion from the last glandular region (GF)—this stains with iron haematoxylin and is not mucus. It will be remembered that the glands of this last region are thick along the floor and few occur laterally and dorsally. Here the capsule appears to be retained for some time, and its floor is thickened, before it is passed into the lumen of the genital papilla and finally deposited on the weed by the foot. Within the capsule the embryo passes through a veliger stage and hatches as a miniature of the adult.

The young at all stages of development are to be found with the adults in spring, summer and early autumn. During the winter the species is far from its summer abundance and the specimens which have then been collected are not fully grown, their reproductive organs being immature. It would thus appear that, as in the other two genera which have been described, *R. diaphana* is an annual. Its rapid development, which is completed within a fortnight, and its rapid rate of growth, enable it to take advantage of favourable climatic conditions, so that during the spring and summer several generations may be co-existent.

RISSOELLA OPALINA (JEFFREYS)

The semi-transparent and highly glossy shell of *R. opalina* is globular in form (Fig. 6 A). There are three and a half whorls separated by broad deep sutures; from the first, which is low, the shell expands abruptly. The body whorl is rounded and its length is approximately twice that of the short, blunt spire. The mouth is broadly rounded anteriorly and gradually contracts posteriorly; the outer lip is sharp and thin, the inner flexuous and thickened on the lower part of the columella. The empty shell is a pale yellowish brown, though in the living animal it appears darker owing to pigmentation in the underlying tissues. When the animal is expanded, the short, tubular snout (ST) projects from under the anterior edge of the shell; above it, and on each side, is a deeply bifid tentacle (T) which is thickly ciliated. The upper surface of the body is mottled with purplish brown or black except for the tentacles, the V-shaped depression which lies immediately below the mouth and is the opening of the anterior pedal gland, and the periphery of the foot—these three regions are colourless. The eyes (E) are situated on slight protuberances and lie close together beneath the shell from which they are never extended. Each is surrounded by an unpigmented ring of tissue. In the living animal the brown pigment of the mantle can be seen through the shell, varied here and there by lighter wavy streaks and by cells filled with orange spherules. Three dark blotches lying within the mantle constitute one of the most characteristic features of the species and mark the position of groups of glands (PI), which are similar to the single group found near the anus in *R. diaphana*. In the upper coils of the spire the excretory cells of the digestive gland (P) can also be seen through the shell as scattered dark spots. The foot is large and triangular, slightly notched in front with the two anterior angles rounded, and bluntly pointed behind (PF). There are two pedal mucous glands resembling those of *R. diaphana*; the V-shaped depression on the propodium which marks the opening of the anterior one is, however, more pronounced.

The organs associated with the mantle cavity differ in some detail from those which have been described for *R. diaphana*. On the left of the mantle, and in the anterior position, is the rudiment of a ctenidium in the form of a few strongly ciliated folds of epithelium; these help to maintain the pallial water current, though they are of little importance in respiration. To the left of this, and washed by the inhalant stream, are the openings of two large multicellular glands, one at the edge of the mantle, and the other just within the mantle cavity, around them stretching a patch of epithelial mucous cells. Each opening leads back through a ciliated and glandular duct to the more posterior gland which lies where the mantle separates from the rest of the body. The gland which opens at the edge of the mantle is composed of mucous cells; the second, opening just within the mantle cavity, is surrounded by minute black pigment granules, and these may also be scattered between the large gland cells.

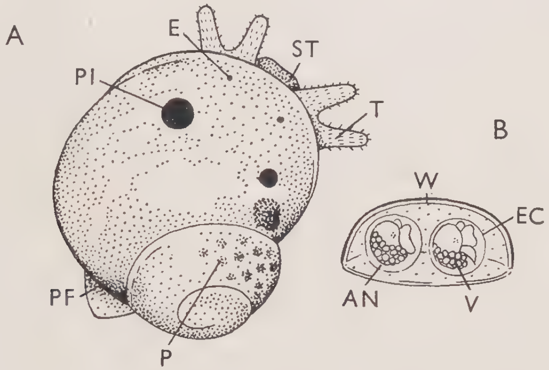


Fig. 6. *Rissoella opalina*. A. Living animal, ×40. B. Egg capsule, ×37. P, spherules in excretory cells of digestive gland; PF, posterior tip of foot; PI, pigmented group of gland cells; V, veliger. Other letters as in Figs. 1 and 5.

This gland is one of the three dark blotches which are conspicuous through the transparent shell. Median to the rudiment of the ctenidium is the anterior limit of the kidney which lies within the mantle, and is separated from the mantle cavity by a layer of squamous epithelium. This part of the mantle, within which lies the kidney with its rich vascular supply, is presumably the chief respiratory surface. The hypobranchial gland is, as in *Omalogyra* and *Rissoella diaphana*, displaced to the right owing to the interpolation of the kidney between the ctenidium and the gland. It stretches back from the opening of the mantle cavity to about the level of the anus—on the median side it abuts against the right wall of the kidney, and laterally against the columnar ciliated epithelium which lines the exhalant opening. Anterior to the anus opens the second of the three groups of large gland cells. This one, embedded in the mantle, is smaller and in a position comparable to the similar gland in *R. diaphana*. From just posterior to the anus a tongue-like projection of the mantle wall juts forwards ventral to the opening, so that the faeces are discharged into a special compartment of the mantle cavity lying between this on the left side and the mantle itself on the right. Along each side of the compartment, on the surfaces facing one another, is a short strip of ciliated epithelium which drives the faecal matter forwards. Unlike *R. diaphana* the strips are short, since the anus is farther forward, and they do not enter the rectum itself. Embedded in the projection, and opening on its ventral surface posterior to the anus, is the third group of large pigmented glands. The only apparent function of these glands is to compensate for the reduced size of the hypobranchial gland and the lack of intestinal glands to consolidate the faeces. Posteriorly the mantle cavity is filled by the pallial oviduct, which projects from the dorsal wall of the body.

The internal anatomy of *R. opalina* is sufficiently similar to that of *R. diaphana* for a description to be unwarranted. The alimentary canal is built on the same plan, and the histology of the digestive gland, and its mode of functioning, is similar. In the reproductive organs there are some differences in detail, though as far as the functioning of the organs is concerned these are insignificant. One point which deserves mention is the absence of the modified receptaculum seminis which in *R. diaphana* serves as a reservoir for unwanted secretion and sperm.

Reproduction and Life History

The egg capsules of *R. opalina* have not previously been described. They are laid during the spring and summer months on green and red algae. The ten capsules which have been investigated contained either two, or rarely (twice) three, embryos, each in an individual mass of albumen which is surrounded by an egg covering. The embryos, with these protective layers, float in a common fluid which fills the capsule. The capsule is hemispherical, with the flattened surface, attached to the weed, measuring approximately 0·65 × 0·4 mm.; the height is about 0·5 mm. The wall is thick, semi-transparent and of a fibrous texture, being composed of conchiolin threads in a mucoid substrate. It is produced by the composite secretion from the capsule gland. The method by which the capsule is manufactured in the pallial oviduct is similar to that of *R. diaphana*.

The embryos pass through a veliger stage and develop to a replica of the parent before they hatch. The full development in the summer months takes about a fortnight. During this time the embryo comes to occupy the entire space within the egg covering, which appears to be stretched during its growth; the covering is not broken until the young are ready to escape from the capsule. The veligers can be recognized by the early appearance of the groups of large pigmented gland cells which lie in the mantle. Also through the mantle, at a later stage in embryonic life, the kidney tissue can be seen.

Young, which hatched from capsules during August, ranged from 0·18 to 0·27 mm. long. They adopt the same feeding habits as their parents and within a fortnight their size is more than doubled (0·43–0·68 mm.). Breeding is continuous throughout the warmer months when individuals at all stages of maturity can be found in the rock pools in comparative abundance. The adults with very few exceptions do not survive the winter, when the number of the species is low, and an immature, slow-growing population is characteristic.

Discussion

Skeneopsis planorbis, *Omalogyra atomus*, *Rissoella diaphana* and *R. opalina* are amongst the smallest British marine molluscs and are inhabitants of rock pools below the level of mid-tide, especially those which have an abundant growth of algae. They are rarely found elsewhere on the shore. As compared with the more familiar and larger intertidal prosobranchs these small forms show in some respects a simplicity of structure, and in many others a high degree of specialization. The latter may be correlated both with their habitat and their smallness.

All four species are herbivorous, feeding on diatoms, algal filaments and some detritus, and during the warmer and lighter months of the year, when conditions favour plant growth, they feed continuously, even at low tide when other herbivores, uncovered by water, are less active. There appears to be no cellulase in the digestive system, since uninjured plant cells pass through the gut undigested, and add to the abundant faecal matter. Nevertheless, unlike other herbivorous intertidal prosobranchs, the intestine is extremely short: in *Omalogyra* the length is one-third the length of that part of the gut lying anterior to the ducts of the digestive gland, whereas in the limpet the corresponding proportion is 8:1. The limpet is uncovered by the tide for a considerable number of hours each day, and the faecal matter must then be stored in the long glandular intestine where it is elaborated to prevent fouling of the mantle cavity later (Graham, 1932). Molluscs like *Skeneopsis*, *Omalogyra* and *Rissoella*, which live predominantly in rock pools, need none of these precautions, since there is a continuous flow of water through the mantle cavity to carry away the faeces, and a short and histologically simple intestine suffices when its function is simply one of transport. The intestine does not enter the coils of the visceral mass, but, from the anterior region of the stomach, at the posterior end of the body whorl, it passes directly along the right side of the mantle to the anus. Moreover, in *Omalogyra* and *Rissoella diaphana*, and to a lesser extent in *R. opalina* and *Skeneopsis*, it becomes shorter still because of the posterior position of the anus, which lies deep in the mantle cavity instead of at its opening.

It is a well-known fact that certain prosobranchs lose their ctenidium. In *Pomatias elegans*, and perhaps also in *Acicula lineata*, this is associated with a change from an aquatic to a terrestrial habitat. It would seem that smallness is a factor leading to the same result, since in the Omalogyridae, Rissoellidae and Pyramidellidae there is no gill. The loss of a special respiratory surface in the minute representatives of a phylum is, of course, a common occurrence. It is probable that a certain amount of respiratory activity is normally carried out by the mantle in any mollusc, and it would appear that this is adequate for the respiratory needs of animals of such small size as those which are mentioned above. Three of the four species which have been described show other changes in the organs associated with the mantle cavity, which may accompany this loss. *Skeneopsis*, which is larger than the others, retains to a greater extent the typical arrangement of organs in the pallial cavity: it still possesses a ctenidium, though the number of filaments is reduced to nine, the kidney lies near the posterior end of the mantle cavity and the hypobranchial gland extends far back along the right side. In *Rissoella diaphana* and *R. opalina* the ctenidium is represented only by a patch of ciliated columnar cells, and in *Omalogyra* it is lost entirely. In these three the kidney has grown forwards mid-dorsally into the mantle, and brings with it a rich vascular network, which is separated from the water current in the mantle cavity only by a squamous epithelium. This, perhaps, increases the chances for the oxygenation of the blood. It is tempting to imagine that the similar forward thrust of the kidney in the other gastropods without a gill—the pulmonates and *Pomatias elegans*—may confer a similar benefit upon the animal. In *Omalogyra* and *Rissoella* the hypobranchial gland does not spread far beyond the anus, but its small area may perhaps be compensated for by the relatively enormous size of some individual cells. Accompanying the gland are longitudinal strips of columnar ciliated epithelium which pass forwards from the anus and produce a strong exhalant current. This current induces the inhalant flow of water along the right side of the mantle cavity, which is normally maintained by the ctenidium.

The ability of these gastropods to produce vast quantities of mucus from the foot would appear to be associated with their habitat. In the calm waters of a rock pool at low tide, they can utilize the mucous rope played out from the posterior pedal gland to lower themselves through the water in a caterpillar-like fashion. When the tide is high, and the water more turbulent, the viscid secretion from the gland, as well as from the general surface of the sole, helps them to maintain a firm hold. The posterior pedal gland has already been described in the rissoids (Johansson, 1939), and it occurs in other small, intertidal gastropods such as *Bittium*, *Cerithiopsis* and *Triphora* (personal observation). As a result of this excessive demand for mucus the glandular tissue has become too extensive to be accommodated entirely within the foot, and spreads into the haemocoel along each side of the buccal cavity and the anterior oesophagus.

As far as the internal anatomy is concerned there are two main points worthy of notice: the simplicity of the gut, and the complexity of the reproductive organs. The oesophagus differs from that of the typical prosobranch in being devoid of oesophageal glands. In the related Rissoidae the explanation of this seems to be the presence of a crystalline style in the stomach. None of the creatures under consideration possesses such a structure, so that the simplification of the oesophagus must be due to something else. Now this part of the alimentary canal runs through the connexion between head, foot and visceral hump, where space has to be made for large and complex reproductive ducts which spread into all available corners, and it is probable that the presence of these limits the size of the oesophagus. Digestive tissue is, therefore, confined to the digestive gland which completely fills the visceral hump, except for the gonad, and its extent in *Omalogyra* is increased by spreading on to the gastric wall, and in the winter form—a particularly small animal—on to the lateral walls of the oesophagus as well. The epithelium in the digestive gland is composed of (*a*) digestive cells, (*b*) lime cells, and, except in *Omalogyra*, (*c*) cells which appear to act as deposits for excretory material. I have never observed this to be eliminated, and it would appear that these cells act as a kidney of accumulation, which is a perfectly feasible arrangement in an annual mollusc. This would also have the effect of relieving the kidney itself of a great deal of its normal work, leading to a simple sac-like structure, suggesting, in fact, that the organ has become more important from the respiratory than the excretory point of view. It may still, however, be required for osmoregulatory purposes, which may, at times, be a matter of prime importance to an inhabitant of a rock pool.

The survival of these rock-pool prosobranchs depends upon their ability to take advantage of conditions which favour their rapid growth and reproduction. These are fulfilled during the warmer months of the year by the high temperatures and ample food supply. The population is then at a maximum, and several generations of each species may be co-existent. With the fall in temperature during the autumn both growth and reproduction are retarded, and the mature population gradually dies out, so that only perhaps an occasional individual will survive into the winter. The population is then at a minimum: it is typically immature, having been derived from eggs laid by late spawners, and the growth of the individual is extremely slow compared with that during the summer. The necessity for a rapid increase in numbers is reflected in the hypertrophy and complexity of the reproductive organs to provide for the protection and feeding of the embryos. Relatively large egg capsules are produced; each is fixed to the weed on which the animals live and contains one to three heavily yolked eggs, surrounded by albumen, and protected by a thick wall. The development takes about a fortnight during a favourable summer and the young hatch as miniatures of the adult. If conditions are good, they grow rapidly, mature, and reproduce in the same season—*Omalogyra* may develop from the egg and reproduce in about 7 weeks. The life of such individuals is short and may be reduced to less than 6 months.

A similar maximum of numbers during the summer is found in *Rissoa parva* (da Costa), and probably many other rissoids. In these, however, some mature animals may live through the winter, spawning the while.

Rissoella and *Omalogyra* are hermaphrodite and ripe spermatozoa and ova occur simultaneously. Simultaneous hermaphroditism is a fairly common phenomenon within the prosobranchs, and is found in quite unrelated forms—*Valvata*, *Velutina*, *Cerithiopsis* (personal observation) and in all the Pyramidellidae. Little is known of the extent to which self-fertilization is practised. It seems likely that it takes place in *Omalogyra*, and there is no morphological bar to its accomplishment in *Rissoella*. In *Omalogyra* there does not appear to be anything which could act as a copulatory organ in the summer population, in which the development of the reproductive organs is different from that of winter forms, yet, despite this, reproduction goes on rapidly, and the explanation may be self-fertilization or parthenogenesis, but the latter seems far less probable. In individuals which develop slowly during the winter months and which come to maturity in the spring, the male system is the first to become functional, and it seems likely that copulation will then occur, but, as I have never seen this taking place, I do not know whether it is a reciprocal act or not.

If the hermaphrodite reproductive system be neglected, it would appear that the anatomy and life history of the molluscs under discussion indicate a relationship with the Rissoidae. Many of the rissoids are intertidal, or inhabit shallow waters, and they also possess a posterior pedal gland which extends from the foot into the haemocoel of the head; to them such a gland is as useful an aid to locomotion as it is to *Skeneopsis* and *Rissoella* and enables them to exploit the surface film as well as the substratum. The food and feeding habits are also similar—except in *Omalogyra*. The food consists of algal filaments, diatoms and detritus. It is passed down a simple oesophagus, which lacks glandular pouches, and is partly digested in the capacious stomach. Amongst the rissoids several species (Graham, 1939; Johansson, 1939) possess a crystalline style, which, however, is not present in *Skeneopsis* and *Rissoella*. In *Omalogyra* the radula is reduced to three teeth in each row (Ankel, 1936) which puncture the algal cells from which the sap is sucked. Pruvot-Fol (1926) points out the similarities between the structure and function of this radula and that of the ascoglossan nudibranchs, and even goes so far as to suggest the presence of an ascus sac for used teeth in *Omalogyra*, though I have never seen anything of this nature. Her final conclusion is that the similarity is entirely due to convergence. The egg capsules of the rissoids are fixed on weed and are similar in most respects to those of *Skeneopsis*, though they contain relatively smaller and more numerous eggs which escape as free veligers (Lebour, 1934). Thus in the rissoids the general parallelism is maintained between lack of specialization in bodily structure and simplicity of larval history. Related to the rissoids are the hydrobiids amongst which *Hydrobia jenkinsi* Smith is peculiar in practising parthenogenesis. In other species of *Hydrobia* the sexes are separate, so that parthenogenesis in *H. jenkinsi* would appear to have arisen by the loss of the male. *Omalogyra* may indicate a different way in which a purely parthenogenetic species may evolve—that is by the reduction and final loss of the male stage in the reproductive activities of a hermaphrodite.

SUMMARY

The external features of *Skeneopsis planorbis* (Fabricius) are described and compared with those of *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *R. opalina* (Jeffreys).

The foot has a large posterior mucous gland (Figs. 1 and 4, PM; Pl. IV, figs. 1 and 2, AL, PL), its secretion forming a thread on which the mollusc can climb from one level to another.

Correlated with their small size are modifications of the pallial organs. *Skeneopsis*, the largest and least specialized, has a bipectinate osphradium, but the gill is reduced to nine filaments; the anus lies well within the mantle cavity. In the other genera osphradium and ctenidium are lost, though the latter may be represented in *Rissoella* by a small tract of ciliated epithelium. In the absence of a ctenidium the animals depend entirely upon pallial respiration and the stream of water through the mantle cavity is maintained by other means: from the anus strips of ciliated epithelium pass forward to the mouth of the mantle cavity, causing a strong exhalant stream and carrying away the faecal pellets. There is a compensating inhalant flow. The kidney (Pl. IV, figs. 1 and 2, K), with its rich vascular supply, has migrated into the tissues of the mantle, increasing its respiratory efficiency.

In the internal anatomy the simplicity of the gut and the complexity of the reproductive organs are the most outstanding features. One may be the cause of the other (pp. 628–29).

The animals are abundant during the warmer months and scarce in winter, when an immature slow-growing population is found. The opportunity for rapid increase in numbers during spring and summer is given by the hypertrophy and complexity of the reproductive organs which provide for the protection and feeding of the embryos.

Omalogyra and *Rissoella* are hermaphrodite. It seems likely that self-fertilization may occur in the summer animals of *Omalogyra* in which there appears to be no copulatory organ. Summer individuals differ in other structural details from the winter animals. In *Rissoella* there is no morphological bar to self-fertilization, but it has never been observed.

Egg capsules (Figs. 1 and 6) are fixed to weed and contain from one to three eggs, which hatch in about a fortnight at summer temperatures. The young escape in the crawling stage, and, if conditions are favourable, become mature in 6 weeks or less and reproduce in the same season. Thus one generation follows rapidly upon another.

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THE GONADS, LARVAE, AND BUDDING OF THE POLYSTYELID ASCIDIANS *STOLONICA* AND *DISTOMUS*

By N. J. Berrill

From the Plymouth Laboratory and McGill University, Montreal

(Text-figs. 1–6)

Stolonica socialis (Hartmeyer) and *Distomus variolosus* Gaertner are two species of styelid ascidians with a capacity for budding and colony formation, found on both sides of the western end of the English Channel. *Distomus* occurs immediately below the level of extreme low spring tides, commonly encrusting the sides of rocks and laminarian bases. *Stolonica* is more usually found by dredging in deeper water, on the upper sides of stones or gravel bottom. Their external appearance and general internal anatomy have been well described and beautifully illustrated in the monograph of Lacaze-Duthiers and Delage (1892), while the process of budding has been investigated by Selys-Longchamps (1917).

In spite of their local abundance and striking appearance, little attention has been given them by English biologists and much of general interest has been overlooked, while an over-emphasis of the importance of the pattern systems of botryllid colonies has masked the close relationship of all the budding styelid-like ascidians. This relationship is discussed further, after descriptions have been given of the breeding cycles of *Stolonica* and *Distomus*.

Stolonica socialis (Hartmeyer)

Mature colonies (Fig. 1 A) consist of loosely associated individuals from 10 to 15 mm. high, of a bright yellow-orange when alive, each with independent branchial and atrial siphons.

With regard to the internal anatomy (Fig. 1 B) the main points of interest are that the branchial sac has three true moderately well-developed branchial folds on each side. The heart has one end opening, as in many other ascidians, at the posterior end of the endostyle. A considerable part of the tubular heart extends anteriorly and mid-ventrally, immediately below the endostyle. The neural gland is dorsal to the ganglion. The most striking feature, however, is the distribution and nature of the gonads.

Gonads

The gonads (Fig. 1 B—D) are arranged in three rows, one along each side of the endostyle, and one on the left following the outer course of the intestine. They are essentially hermaphrodite organs imbedded in the atrial or mantle wall. Each testis and ovary has its own duct extending as part of the atrial lining, opening into the atrial cavity.

The fully formed gonad consists of a testis divided into from six to a dozen lobes all emptying into a common sperm duct which projects into the atrial cavity within a long slender extension of the inner atrial wall, and an ovary with a single large ovum and several small oocytes, with a very short and very wide oviduct opening to the atrial cavity.

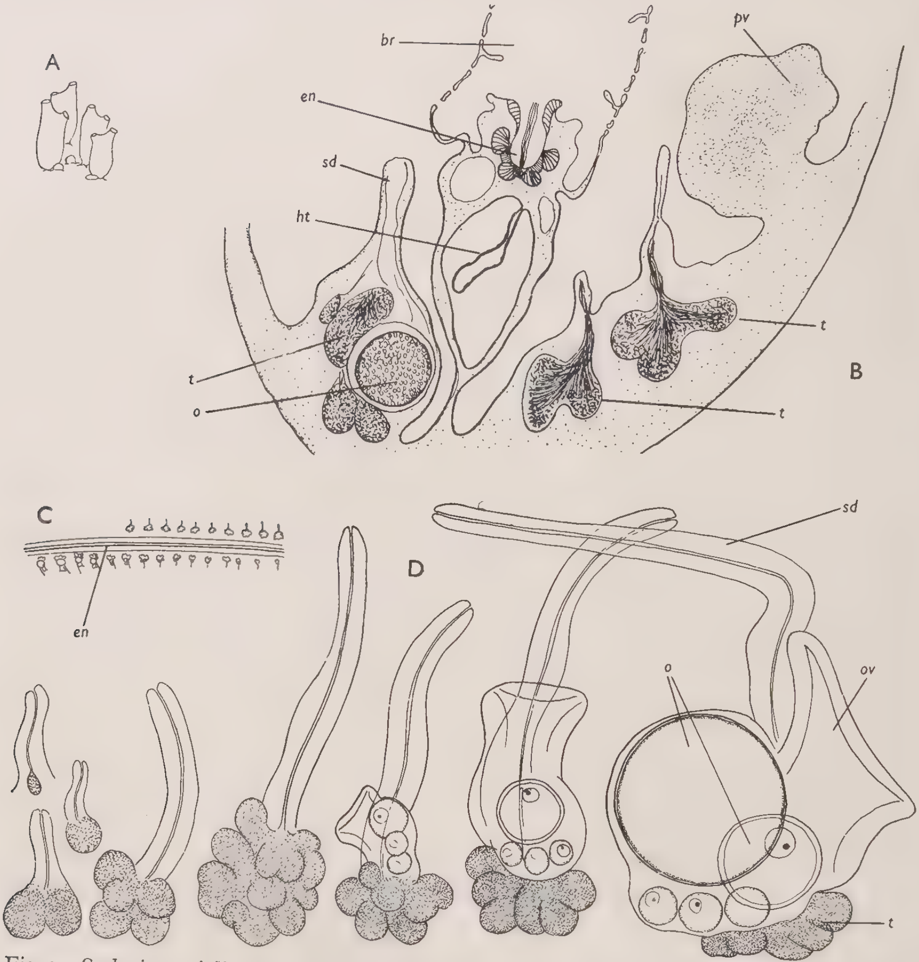

Fig. 1. *Stolonica socialis*. A, zooids. B, cross-section of mature zooid to show position of heart ventral to the endostyle, and gonads in the mantle wall on each side of the mid-ventral line. C, endostyle with male gonad series on one side and male to hermaphrodite series on the other. D, graded samples of hermaphrodite series. *br*, branchial sac; *en*, endostyle; *ht*, heart; *o*, ripe egg; *ov*, oviduct; *pv*, parietal vesicle or endocarp; *sd*, sperm duct; *t*, testis.

The gonads, however, are not all alike. The series along the right side of the endostyle and the series following the course of the intestine on the left side each consists of testes only, essentially the same as the male component of the hermaphrodite unit just described; while the series along the left side of the endostyle is a graded one, and at its posterior end from four to six units are hermaphrodite, each with a fully grown ovum (Fig. 1 C). At the anterior end only male components are present, those at the extreme anterior end being relatively extremely small. Intermediate units occur along the middle range of the series.

As the male gonads become progressively smaller it is evident that the number of the testis follicles is correspondingly reduced, the size of the individual follicle remaining unaffected until the number is reduced to one, and only further diminution results in a reduced follicle size. Also the length of the sperm tube is directly proportionate to the number of follicles or mass of testis tissue.

The size of the male gonad increases until a maximum is reached approximately midway along the side, after which it remains virtually the same size, although there is some indication of further but slight increase. The female gonad first appears about halfway along the series as a group of small partly grown ova associated with a relatively small oviduct. The size of the unit increases progressively, passing towards the posterior end, until a maximum size is reached about one-quarter the length of the series from its end. The maximum units have a fully grown ovum, one partly grown, and several oocytes showing no sign of growth at all. The smaller units may have a partly grown ovum and undeveloped oocytes, but no fully grown ovum.

The series, which is illustrated in Fig. 1 D, may accordingly be regarded as a single series of increasing unit sizes, progressive size increases giving rise to progressively larger male gonads until a maximum is attained, further size increases resulting in first rudimentary and finally large functional female gonads.

The male series on the right of the endostyle and alongside the intestine exhibits less of a size gradient and its members do not attain the tissue mass of the hermaphrodites. It is believed that unless the initial rudiment of a gonad exceeds a certain critical size, it will not grow to a size capable of forming or segregating oocytes, and unless oocytes are formed no oviduct will develop.

The majority of the middle zone hermaphrodites probably do not mature as female gonads, since, shortly after the maximum gonads have shed their eggs and the tadpoles developed, the parent zooid becomes senescent and is sloughed off. As far as can be determined the maximum gonads at the posterior end of the series each yield two ripe eggs in the course of the breeding season, three at the most and one at a time. The submaximal gonads produce but one ripe egg coinciding with the shedding of the last egg of the larger units, while the smaller units near the beginning of the hermaphrodite series fail to produce any. Whether, given sufficient time, they could do so is not known, for their time is cut short by the death of the whole organism.

Development of the Egg

Development of the egg as far as the formation of the active tadpole larva takes place within the atrial cavity. The mature eggs are the largest, though not the yolkiest, known among ascidians, with a diameter of approximately 0·70 mm. They are equalled in size only by those of *Ecteinascidia turbinatum* Herdman.

Cleavage is unmodified, with the same sequence of pattern established for *Styela* by Conklin (1905). Gastrulation occurs between the sixth and seventh cleavage as in all other ascidians and is typically embolic. In spite of the large size of the egg and its rather heavy yolk content, the yolk is distributed as in smaller and less yolky eggs and has no apparent affect upon either cleavage or gastrulation, other than a general retardation of developmental rate (Fig. 2 A).

At 16° C. the tadpole hatches by digestion of the egg membrane about 5 days after fertilization, although at that time it is still inactive. It continues development for another 4 days within the atrial cavity of the parent before it attains functional differentiation and is liberated. During this last period there is considerable growth of the trunk, while the changes in the tail are mainly those of fine differentiation of the locomotory tissues. The free-swimming period usually lasts about 2 days, but may be shorter or considerably longer. It may be greatly affected by the length of time the fully formed tadpole has been retained within the parental atrial chamber. The heart commences beating about 4 days after the tadpole first becomes attached, the four rows of gill slits function 2 days later, and the gut functions fully after another 5 days. It is this last state (Fig. 2 B) that should be regarded as the end of egg development, and not the attainment of the active tadpole stage.

Tadpole Larva

The tadpole (Fig. 2 B) is about the largest and most effective swimmer among ascidian larvae. The trunk is approximately 1 mm. and the tail, exclusive of the cuticular fin, 2 mm. long. At a temperature of 16–17° C. the tadpole has a free-swimming period of from 24 to 48 hr. for the great majority. Swimming is somewhat intermittent under laboratory conditions, depending greatly upon external stimulation. At this temperature the stroke of the tail is about 8–12 per sec., and progress about 25–30 mm. per sec. Tadpoles show response both to light and gravity, being positively heliotropic and negatively geotropic during the first few hours at least.

During the active phase the trunk remains ovoid and streamlined. The tail fin, a cuticular secretion, is vertical, retaining the primitive position in spite of the large size of the egg, and as the result of the developing tail being coiled horizontally around the trunk rather than vertically. Both branchial and atrial invaginations are formed at this time, the atrial being median and single from

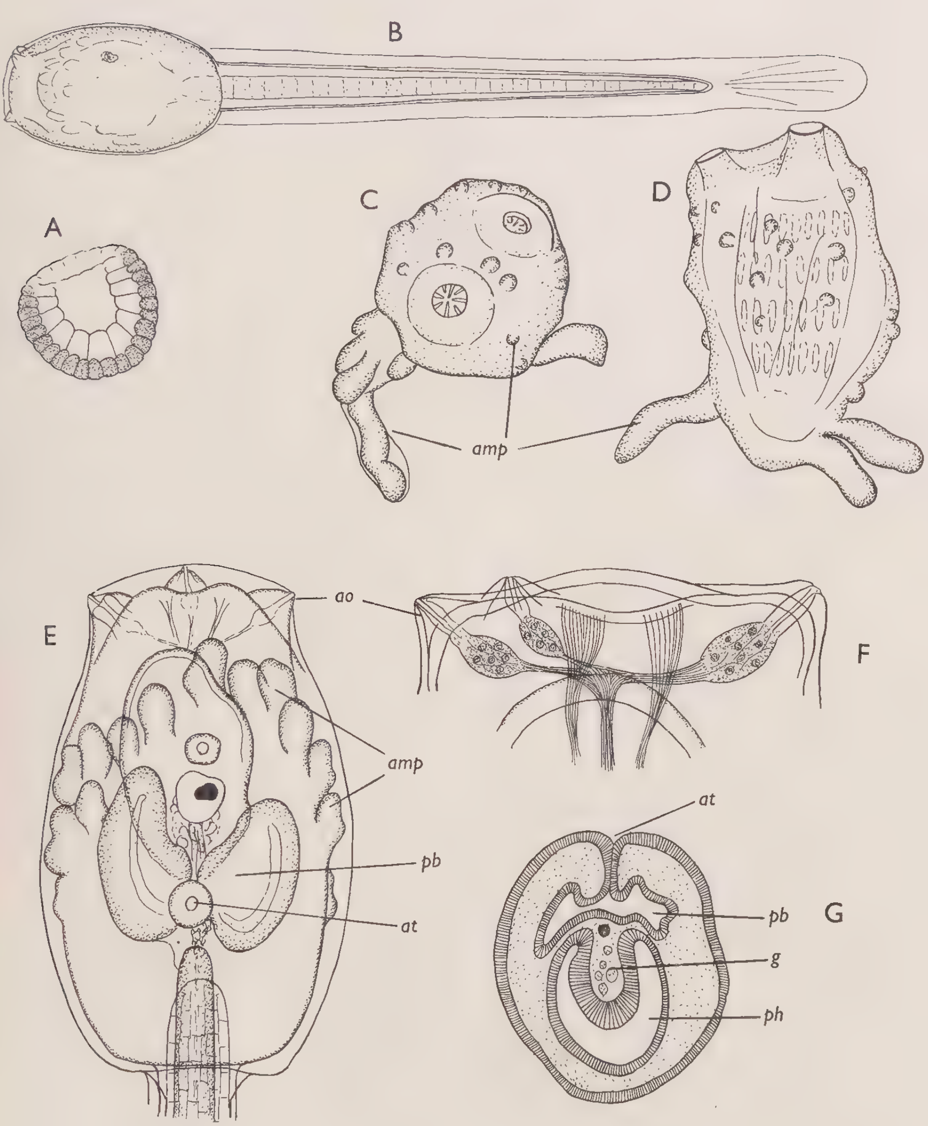

Fig. 2. Development and tadpole structure of *Stolonica*. A, gastrula. B, active tadpole. C, metamorphosed individual with siphons open. D, fully developed oozooid with four rows of gill slits. E, trunk of tadpole from dorsal side showing adhesive organs, ampullae, sensory vesicle and peribranchial sacs. F, anterior region of tadpole showing nerves and ganglia to adhesive organs and anterior epidermis. G, cross-section of tadpole through atrial invagination to show ectodermal origin of peribranchial sacs. *amp*, ampulla; *ao*, adhesive organ; *at*, atrial siphon; *g*, ganglion; *pb*, peribranchial sac; *ph*, pharynx.

the first and dividing over the nerve cord to form the peribranchial sacs. Epidermal ampullae are short and numerous and form an irregular circular zone in the front half of the trunk.

Anteriorly there are the usual three adhesive organs (Fig. 2 E). They are relatively simple, though large, forming conical projections distributed in a triangular manner relative to each other. Each is supplied with a ganglion at its base, the nerve fibres from the three uniting to form a single fibre that passes back to the cerebral ganglion (Fig. 2 F). It is accompanied but not joined by a pair of nerve fibres uniting the cerebral ganglion with the mid-anterior epidermis.

The sensory vesicle lies between the two siphons. It is characterized by the presence of a single composite sense-organ (Fig. 3 E) sensitive to both light and gravity, of a type first described by Grave & Woodbridge (1924) for *Botryllus* and named 'photolith' by Garstang & Garstang (1928). Two stages in its development in *Stolonica* are illustrated (Fig. 3, C–F). In the early tadpole a single-celled otolith develops from the floor of the sensory vesicle and appears to be in no way different from the otolith of ascidian tadpoles in general. In the late tadpole, after hatching but before liberation, the pigmented mass of the otolith becomes partly hollowed out, partly extended, to embrace a group of neurosensory cells growing out from the sensory ganglion at the posterior wall of the sensory vesicle. The nuclei and cell bodies of these neurosensory cells for the main part lie outside the pigmented cup thus formed, but rod-like extensions penetrate the dark mass.

The tail is notable for several features. The notochord cells, about forty, in spite of their great size, appear to be but moderately vacuolated, are congested with yolk granules, and maintain their individual integrity throughout larval life. They can be readily identified even later when resorbed and separated in the body spaces of the trunk.

The muscle cells are arranged in two bands, one along each side of the notochord (Fig. 3 A). Each band contains approximately twenty-four cells along its length, and tapers from six to two cells in width from the base of the tail to its tip. The muscle bands do not quite extend to the tip of the notochord. Each muscle cell consists of a central endoplasmic region containing the nucleus, and a relatively clear cortical zone developed equally well on all sides and in which the contractile myofibrillae are formed. Even after metamorphosis, these cells and their zones are recognizable in the resorbed tissue. The most striking feature is the continuity of the myofibrillae from cell to cell (Fig. 3 B). The myofibrils pass as continuous structures, following a slightly spiral course, from the broad base to the narrow tip of the muscle band as a whole, and there is no doubt that the band functions as a unit. The fibrils pass from cell to cell in the cortical or ectoplasmic zone, and there is a definite superficial syncitial or symplasmic state of the tissue. A similar condition has been described by Caswell Grave (1921) for *Amaroucium*, and by Conklin

(1931) for *Styela*. *Stolonica* tadpoles are exceptionally favourable for demonstrating this condition, owing to the large size of the muscle cells and relatively enormous thickness of their hyaline zone.

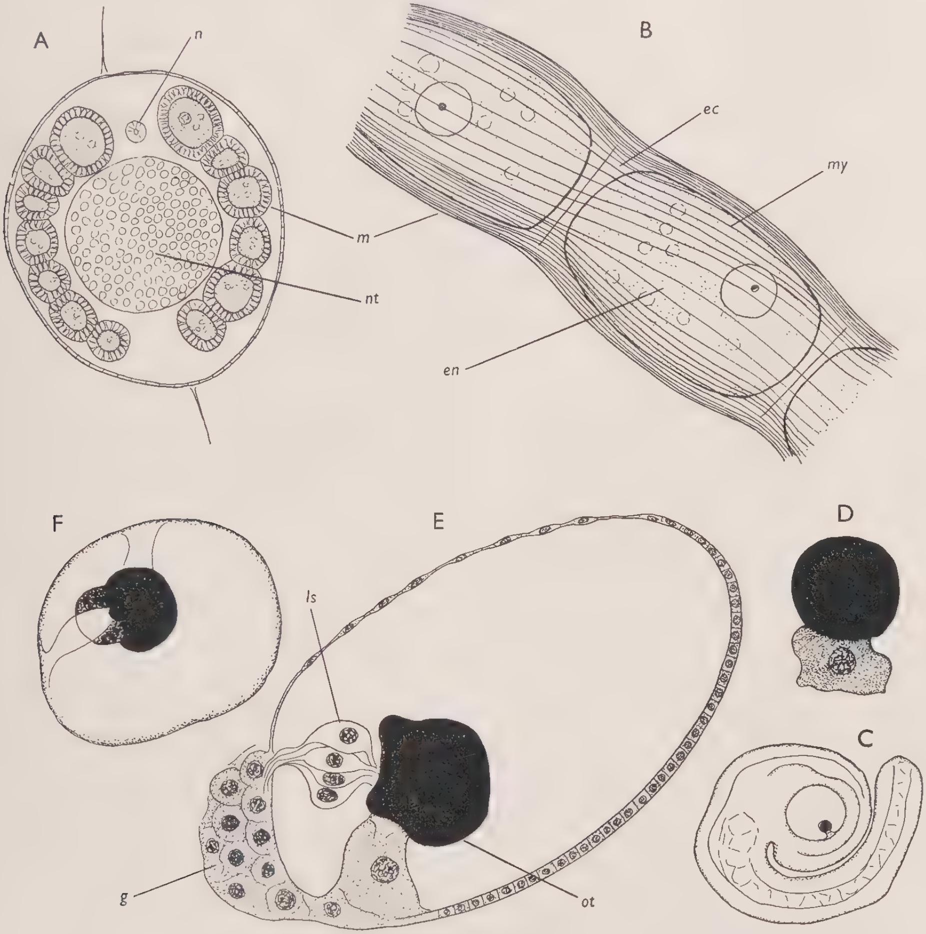

Fig. 3. Tail and sensory vesicle of *Stolonica* tadpole. A, cross-section of tail showing organization of muscle cells. B, adjacent muscle cells showing thick ectoplasmic zone and continuity of myofibrillae from cell to cell. C, embryonic tadpole with newly formed otolith. D, otolith of C at same magnification as figure E. E, sensory vesicle with otolith invaded by light-sensitive neurons to form 'photolith'. F, dorsal view of vesicle showing extension of otolith pigment. *ec*, ectoplasm; *en*, endoplasm; *g*, ganglion; *ls*, light-sensitive cells; *m*, muscle cell; *my*, myofibril; *n*, neural tube; *nt*, notochord; *ot*, otolith.

Budding

The process of budding has been described at length by Selys-Longchamps (1917), to which little can be added. There is no sign of budding in the oozooid when it first functions with the primary four rows of gill slits (Fig. 2 D, G), nor for several weeks after, during which growth occurred, though not enough to increase the number of rows of gill slits. Selys-Longchamps, however, figures (1917, plate III) a young colony from dredged material consisting of a central oozooid with eleven or twelve rows of gill slits, and with about eight buds at all stages of development from initiation to functional zooids with about ten rows of gill slits. Apart from size it seems evident that the process of budding is essentially the same for colonies old or young. An outgrowth develops from the body wall involving the epidermis, the atrial lining, and the mesenchymal tissue between. The process extends a considerable distance from the parental body, while reserve nutritive cells of the circulating system, pseudovitelline cells, accumulate at the tip between the outer epidermal and inner atrial tubes. The tip of the stolonic outgrowth constricts off after the accumulating vitellus attains a certain mass and cuts off circulation through that region. The bud so isolated then starts to develop, although the process is very slow. Fully mature individuals form a relatively large bud of this type which survives the disappearance of the parent in the late summer and completes its own development by the following spring. The internal atrial vesicle always gives rise to the whole of the new organism with the exception of its epidermis, the intervening vitellus becoming progressively utilized in the process.

DISTOMUS VARIOLOSUS GAERTNER

This species has been described both by Lacaze-Duthiers & Delage (1892) and by Selys-Longchamps (1917) under the name *Heterocarpa glomerata* Alder. Selys-Longchamps considered it to be an absurd obedience to intransigent laws of priority to displace *Heterocarpa* by *Distomus*, but this last name appears at present to be the more widely adopted. The *Allaeocarpa apolis* of Michaelsen (1904) is probably synonymous.

Colonies (Fig. 4 A) differ in appearance from those of *Stolonica* in being brick red in colour, in having the constituent zooids closely packed together to form a continuous leathery layer, and in the smaller maximum size of the individual zooids. Internally, the branchial sac is without true folds, although on each side there are three groups of internal longitudinal bars, undoubtedly the remnants of what were originally three branchial folds (Fig. 4 B). The neural gland is dorsal to the ganglion, while the heart extends anteriorly beneath the endostyle as in *Stolonica*, and as in *Stolonica* the gonads are unique, though in their own way.

Gonads

The zooids, as in almost all ascidians, are functional hermaphrodites, but are peculiar in possessing only testes on the right side and ovaries on the left.

The testes (Fig. 4 C, G) are comparatively simple, the smallest being more or less pear-shaped, larger ones becoming relatively elongated, a maximum

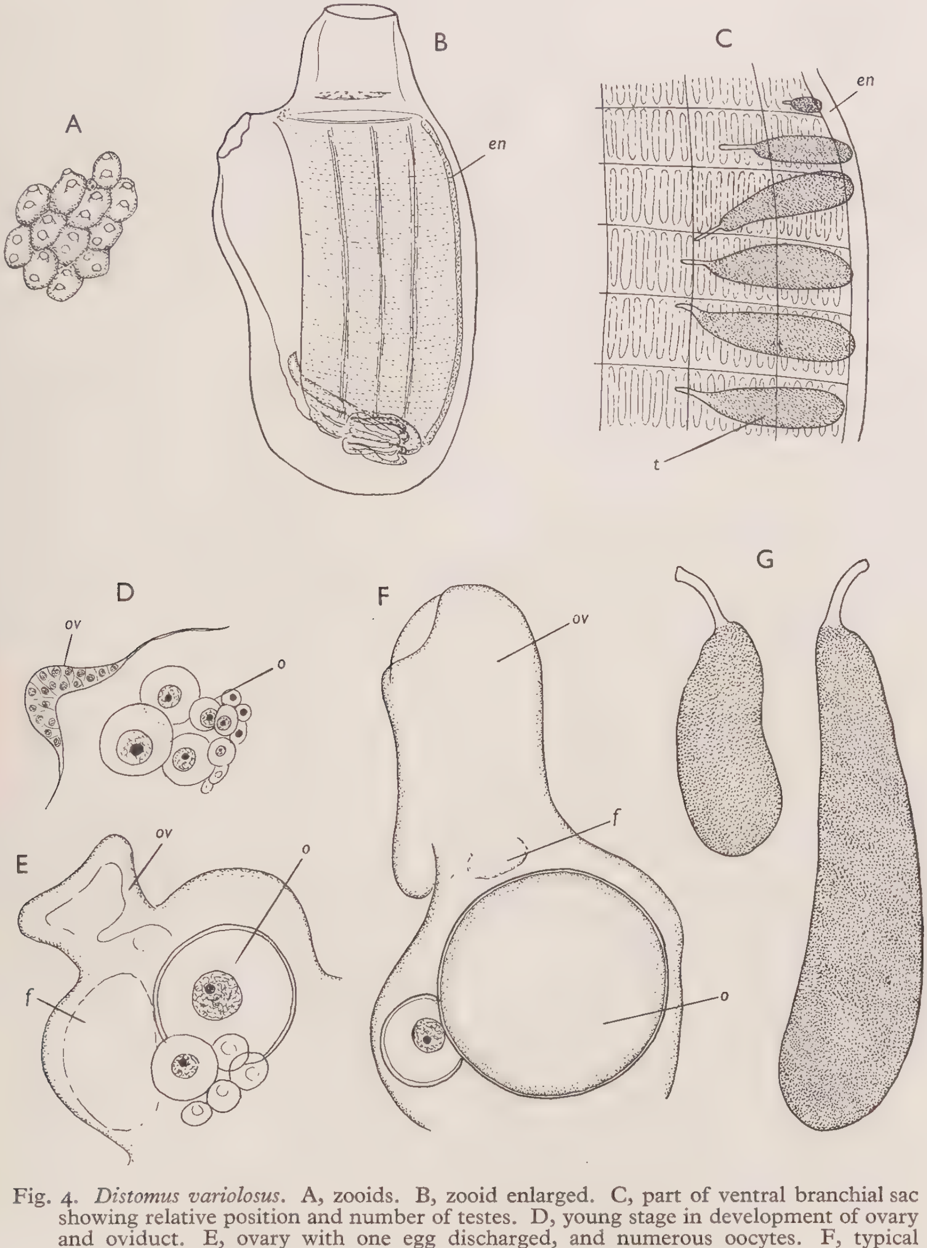

Fig. 4. *Distomus variolosus*. A, zooids. B, zooid enlarged. C, part of ventral branchial sac showing relative position and number of testes. D, young stage in development of ovary and oviduct. E, ovary with one egg discharged, and numerous oocytes. F, typical mature ovary with ripe egg. G, minimum and maximum sized testes. *en*, endostyle; *f*, empty follicle; *o*, ova; *ov*, oviduct; *t*, testis.

width seemingly apparent. The smallest testes occur anteriorly. Usually there is a series of six or seven arranged in the lower mantle wall parallel to the right side of the endostyle, one corresponding fairly closely to each row of gill slits. The short sperm duct of each testis opens towards the dorsal side. There is no trace whatever of an ovary, however rudimentary, in association with the testes.

The ovaries are found in the antero-dorsal mantle wall of the opposite side, and have no trace of a testis associated with them. Three stages in the development of an ovary are illustrated (Fig. 4 D–F). The youngest consists of a group of oocytes and small ova, about a dozen in all, lying beneath the atrial epithelium. The atrial epithelium adjacent to the ovary shows a local thickening protruding into the atrial cavity, foreshadowing the oviduct. The second stage bulges as a whole from the atrial wall and has a moderately large though short and wide oviduct. A half-grown ovum, with a few small ova, are present, together with a recently emptied follicle. The third stage has the fully developed oviduct, a mature ovum, a slightly grown ovum, and an old empty follicle. Only one egg ripens at a time and the gonad has been considered to be a single egg ovary, which it is not. The smallest ova, however, do not have an opportunity to reach the maximum size and it is doubtful whether more than three or at the most four ova mature in the course of the individual zooid's breeding season and cycle.

Development

The ripe egg is a little smaller than that of *Stolonica*, approximately 0·6 mm. diameter. It develops free in the posterior part of the atrial cavity. Gastrulation (Fig. 5 A) is embolic and occurs between the sixth and seventh cleavage. The tadpole hatches from the egg membrane 4–5 days after fertilization at a temperature of 15–16° C. It becomes active and is liberated through the atrial siphon after a further 2–3 days' development. The atrial invagination is single and median-dorsal, and develops after hatching and before liberation.

The free-swimming period for the great majority is from 18 to 30 hr. The stroke of the tail, at 16° C., is 11–14 per sec. and the tadpole progresses 20–25 mm. per sec.

The tail resorbs in the course of about 8 hr. and metamorphosis is complete to the extent of the heart beating and the gill slits functioning 10–12 days after settling. The intestine functions about 2 days later. As in *Stolonica* no protostigmata are formed and four rows of definitive stigmata appear as independent perforations from the beginning (Fig. 5 C).

The tadpole (Fig. 5 B) is large, though not so large as that of *Stolonica*, and is brick red. The cuticular fin of the tail is vertical, the developing tail being coiled horizontally around the embryo, so that it does not become twisted through ninety degrees as it would if the tail retained the primitive vertical position in the limited perivitelline space. A pair of flukes extend posterolaterally from the trunk. They may conceivably have some stabilizing function in swimming. In the anterior half of the trunk a ring of sixteen epidermal ampullae, rarely more, encircle it. The ring is very regular compared with the same feature in tadpoles of *Stolonica*. Three adhesive organs, arranged triangularly, are formed at the anterior tip. During metamorphosis the tail resorbs, the tail cuticle is thrown off, and the trunk shortens along its main axis. At the same time the ring of ampullae extend individually, secreting test substance and making fast to the substratum, taking over the function of the transient adhesive organs.

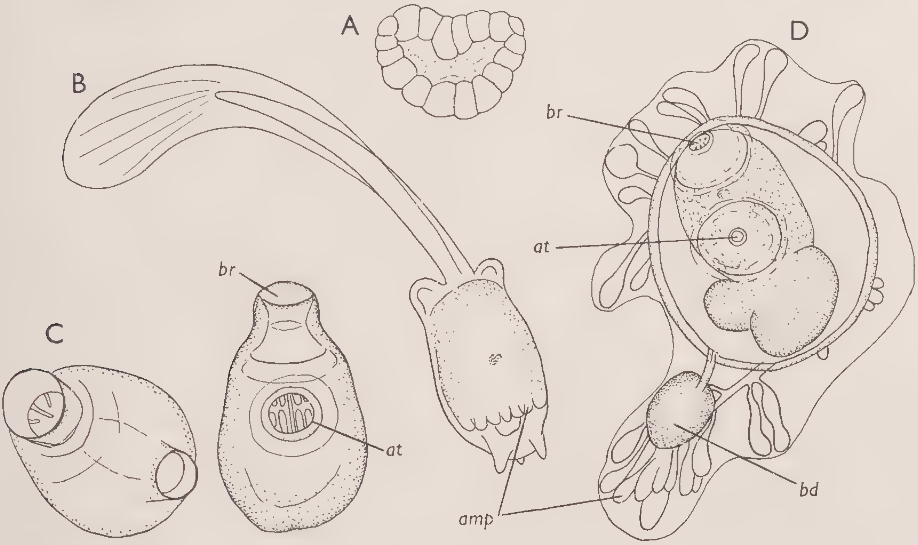

Fig. 5. Development of *Distomus*. A, gastrula. B, active tadpole. C, functional oozooids. D, oozooid after several weeks' growth with first bud and numerous ampullae. *amp*, ampulla; *at*, atrial siphon; *ao*, adhesive organ; *bd*, bud; *br*, branchial siphon.

The adhesive organs are large but simple, consisting of conical epidermal projections containing a hollow core of glandular cells that secrete the adhesive substance. Each has a nerve ganglion associated with its base and a nerve fibre connecting with the central neural ganglion (Fig. 6 E). The fibres remain separate from each other until they reach the sensory vesicle region. Two lateral nerve fibres pass from the central ganglion to a pair of lateral larval ganglia.

The sensory vesicle contains a single sense organ, a typical 'photolith' as in *Stolonica* and *Botryllus* (Fig. 6 D). As in these forms, it develops early as a unicellular otolith from the floor of the sensory vesicle, and late in the course of tadpole development a group of neuro-sensory cells project from the postero-dorsal wall of the vesicle and enter the hollowed-out and extended mass of otolith pigment. The tadpoles are responsive both to light stimuli and gravity.

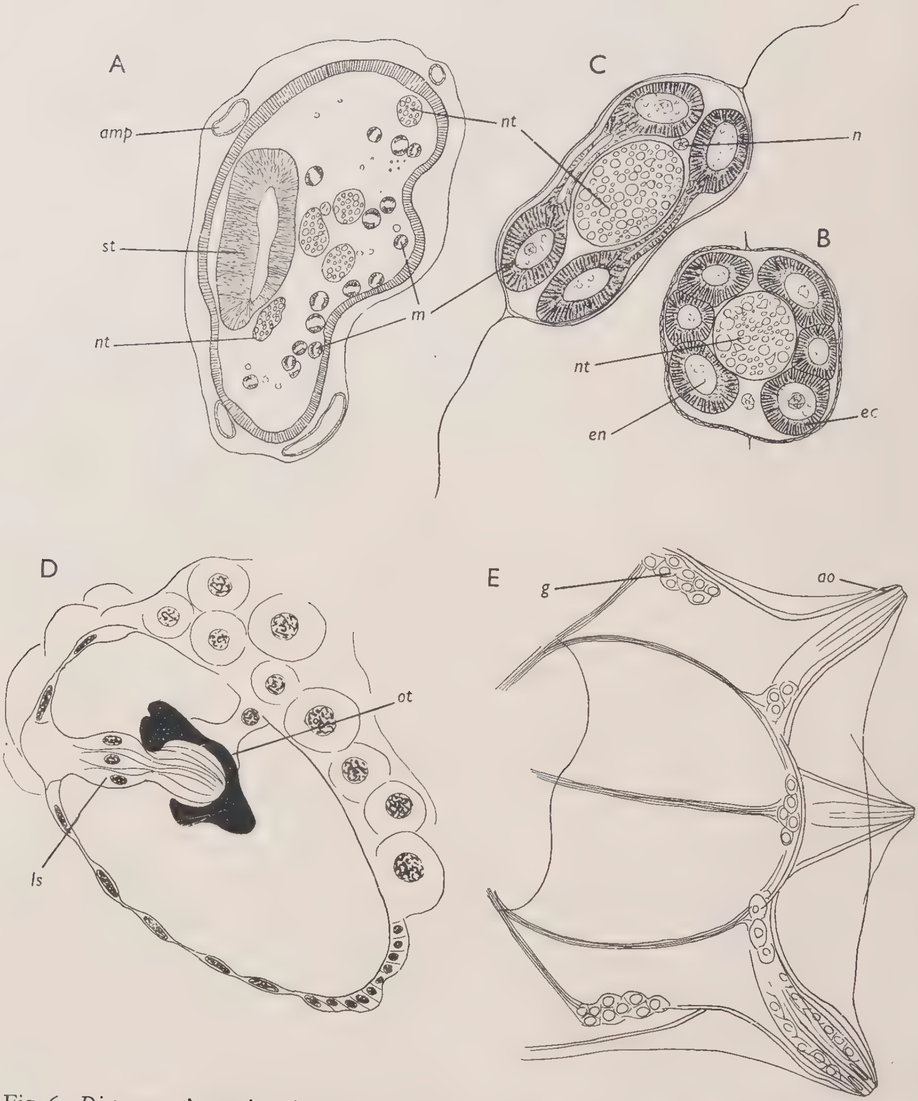

Fig. 6. *Distomus*. A, section through metamorphosed tadpole to show muscle cells and yolky notochord cells scattered through body cavity. B, C, sections of tail through middle and posterior part to show nature and arrangement of muscle cells. D, sensory vesicle with typical photolith. E, anterior region of tadpole showing nerves and ganglia associated with the adhesive organs and anterior ectoderm. *amp*, ampulla; *ao*, adhesive organ; *ec*, ectoplasm; *en*, endoplasm; *g*, ganglion; *ls*, light sensitive cells in photolith; *m*, muscle cell; *n*, neural tube; *nt*, notochord; *ot*, otolith; *st*, stomach.

The notochord consists of approximately forty yolk-laden cells arranged in single series. The muscle cells (Fig. 6 B, C) are arranged in two bands, one on each side of the notochord, each band consisting of three cells in cross-section at the base of the tail, two near the tip. The notochord extends posteriorly slightly beyond the muscle bands. Myofibrillae are continuous from cell to cell throughout the length of the band, taking the same somewhat spiral course as in *Stolonica*. They are confined to the relatively enormously thick hyaline zone. After resorption of the tail, notochord cells still richly laden with yolk granules and muscle cells now isolated and with the fibrilla zone obvious are clearly recognizable scattered through the primary body cavity (Fig. 6 A).

Budding

Buds are produced in essentially the same manner as in *Stolonica*. Local regions of the posterior and ventral body wall, involving epidermis, mesenchyme, and atrial lining, grow out to form the bud stolon. Usually the outgrowth is extremely short and the bud develops at its tip in close conjunction with the parent and without severing its connexion. Winter buds, however, are produced similar to those of *Stolonica*, with large accumulations of pseudovitelline cells between the epidermis and the inner atrial tube. These masses survive the dissolution of the parents after the sexual breeding season and themselves develop to functional maturity by the following spring.

The first buds appear relatively early, from the wall of the oozooid, a few weeks after the settling of the tadpole, at the time the most anterior of the primary four rows of definitive stigmata is dividing into two rows (Fig. 5 D).

Selys-Longchamps (1917, plate III) shows two partly fused young colonies each with an oozooid with about a dozen rows of stigmata, giving rise to five or six buds at various stages. There is evidently a considerable accumulation of reserve cells between the epidermal and atrial layers even in the buds of these early colonies and this appears to be the main source of bud nutrition rather than the communicating stalk with the parent zooid. The epidermis contributes only epidermis, and all other tissues and organs are derived from the atrial epithelium forming the internal vesicle.

THE POLYSTYELID AND BOTRYLLID ASCIDIANS

The most recent systematic treatise on ascidians is the monograph by Van Name (1945) on North and South American forms. In this account the Botryllidae are assigned full family status, but are described as belonging to the same stock as the Styelidae, and as quite closely related to some of the compound members of that family. Van Name is not in favour of separating the compound from the simple Styelidae as a separate family (Polyzoidae, syn. Polystyelinae), as Ärnbäck-Christie-Linde (1923) and others have suggested. Any discussion of such forms as *Stolonica* and *Distomus* therefore involves the botryllids on the one hand and the non-budding styelids on the other.

Van Name's setting apart of the Botryllidae in their old accepted status is based on the presence of zooid systems and common cloacal apertures, and on differences he believes to exist with regard to gonads and budding. His refusal to separate polystyelids from simple styelids is based on the close relationship of *Polyandrocarpa*, a polystyelid, and *Polycarpa* (a simple styelid), when only adult features of the mature isolated individual are contemplated. If only adult characters are considered, there is little doubt that the two forms merit merely a generic distinction.

It is evident that much of the diversity of opinion is due to varying interpretation of similarities in adult and reproductive features. If the classification is to reflect actual relationships, it is important to decide whether similarity of adult structure is basic and other characters convergent, or whether budding and larval characters can be used to unify a group. It is considered here that the last is possible and there is a natural group of styelid ascidians set apart from other styelids by two unique characters, a type of budding and a larval sense-organ not to be found elsewhere among tunicates.

Botryllids and polystyelids are the only members of the order Pleurogona (=Stolidobranchia=Ptychobranchia) that bud. Since no member of this order possesses a posterior abdominal or post-abdominal extension of the body, and the epicardium survives only in one family and as a highly specialized renal organ, there is no possibility of the strobilating epidermal-epicardial budding processes of the Enterogona (=Phlebobranchia+Aplousobranchia), nor is there any structure comparable to the budding stolon of the Perophoridae. The styelid-botryllid type of budding is always fundamentally an outgrowth or outgrowths of the whole body wall at the level of the pharynx, consisting of a hollow protrusion of both epidermal and atrial epithelia with mesenchymatous tissue enclosed between them. It is usually called 'palleal' budding, and the atrial epithelium is invariably the primary morphogenetic tissue. Nothing comparable to this type of budding occurs among any other forms. It accordingly remains to be shown that the marked variability of budding among the botryllids and polystyelids is that of one basic type. There are differences in the number of buds produced; and while in some genera buds may form from a relatively extensive region of the body wall, in others they are localized within a small area on each side. In some forms buds are produced slowly during the long period of growth of the parental individual as a functioning organism, in others either a single pair or a series are formed only during the developmental period of the parent. These variations can be regarded only as specializations in area and time, and do not affect the essential morphology of the process. Morphological differences are not great. They relate to the distance a palleal outgrowth extends before its tip starts to develop as a bud, whether separation of the tip from its stalk is necessary before development starts, and whether nutrition of the buds is effected by a secondary reattachment to a colonial vascular system or is met by accumulation of reserve material between the inner and outer vesicle of the bud. The bud proper always consists of an outer epidermal vesicle enclosing an inner vesicle derived from the atrial epithelium, the latter giving rise to all structures except epidermis.

It is simpler, and therefore more reasonable, to assume that this method of budding has been acquired on a single occasion by the group that exhibits it, than either that it has been acquired more than once or that all pleurogonid ascidians at one time possessed it, and the majority have lost it at different times.

The conclusion that all styelid and botryllid ascidians exhibiting palleal budding comprise a natural group is reinforced by a study of the tadpole larvae. Without exception, every species so far known that forms buds from the atrial body wall produces tadpoles with a 'photolith'. On the other hand, a photolith is not developed in the tadpole of any other ascidian species. All photoliths consist of a single-celled otolith developing from the floor of the sensory vesicle, the pigmented mass becoming hollowed out as a deep cup to receive the distal ends of a group of neurosensory cells growing out from the neural wall of the vesicle in the region where the ocellus occurs in other forms. The organ is responsive both to light and gravity. It is hardly conceivable that parallel evolution would so occur that two or more groups with palleal budding independently evolved a photolith. The coextension of the two features definitely indicates the existence of a single natural group.

At the same time, on the basis of adult structure, the relationship of *Polycarpa* and *Polyandrocarpa* is very close and hardly justifies anything greater than the generic distinction Van Name assigns them. This raises the question whether the Styelidae should be divided into two subfamilies, or whether the budding forms should be raised to full family status. This last may seem more logical, for the polystyelids as a whole exhibit great variability and as a group seem to have been launched on an independent evolutionary career of diversification, but it ignores the obvious relationship with the simple polycarpid styelids. There seems to be little justification for the maintenance of the botryllids, i.e. the genera *Botryllus* and *Botrylloides*, in a separate category, whether family, subfamily or any other, purely on the basis of the presence of zooid systems in the colonies. No such value is given to the presence or absence of systems in other families, e.g. Polyclinidae, and as Brien (1937) has shown they depend on buds being at equivalent developing stages and relatively close together. The striking end-result is out of proportion to the character leading to it. Accordingly the stand taken here is that there is a single natural group, the subfamily Botryllinae, characterized by palleal budding and the presence of a photolith in the tadpole larvae, combining with the Styelinae to form the Styelidae.

It is interesting within this group to try and determine the divergent paths of specialization. Species of *Polyandrocarpa* form a logical starting-point since there is reason to believe the genus is in every way, other than in budding and in the tadpole photolith, merely a slightly dwarfed edition of the styelinid genus *Polycarpa*. In species of both genera there are four well-developed folds of the branchial sac on each side as in styelids generally, and the gonads are hermaphrodite units developing on both sides in the atrial or mantle wall, with eggs and testis follicles numerous in each gland in *Polycarpa* species and the larger species of *Polyandrocarpa*. *Polycarpa* species do not bud, and the tadpoles of all species investigated merely have the unicellular otolith, the ocellus and light responsiveness being absent. *Polyandrocarpa* species produce palleal buds, but belatedly and slowly, so that colonies consist usually of a small number of relatively large zooids. Eggs and tadpoles are larger than those of *Polycarpa* species but smaller than in other polystyelids. In both the smaller *Polycarpa* species (e.g. *P. gracilis*) and larger *Polyandrocarpa* forms (*P. zorritensis*, *tincta*, *gavei*, etc.), the hermaphrodite glands, or polycarps, develop as a series in the mantle wall along each side of the endostyle.

From such a beginning, specializations have occurred more or less independently in three directions, with regard to branchial structure, number and nature of gonads, and time and place of budding.

Budding inevitably leads to a reduction in the size of the zooids, and the more efficient the budding process the smaller the zooids become, since growth is directed more toward zooid multiplication than individual size increase. Colonies with small zooids may therefore have arisen several times within the family, and the secondary simplifications of body structure correlated with size reduction do not necessarily indicate an exclusive close relationship among such forms. In these, the four well-formed branchial folds of *Polyandrocarpa* species are reduced to various degrees.

In the subgenus *Eusynstyela* of *Polyandrocarpa*, zooids do not exceed 10 mm. in length, and reduction is noticeable in the number of longitudinal bars constituting each of the four branchial folds. In *Stolonica* and *Gynandrocarpa* they are similarly reduced, but in addition the number of folds is reduced from four to three. In *Distomus* the three folds are reduced to three groups of longitudinal vessels corresponding to, but not actually forming, folds. Where zooids are even smaller, not more than 5 mm. long, all trace of folds as such is gone, but they are represented by evenly spaced inner longitudinal branchial vessels, 8 in *Polyzoa opuntia*, 5–6 in *Alloeocarpa bacca* and *Metandrocarpa dura*, 4 in *Kukenthalia borealis* and *Symplegma viride*, and 3 in *Polyzoa translucida*, and the species of *Botryllus*, *Botrylloides*, and *Chorizocarpa*. Since there is such a correlation of branchial reduction with reduction in zooid size as a whole, branchial structure by itself cannot be used as a basis for relating species or genera.

With regard to the reproductive organs a somewhat similar situation exists. The first sign of a reduction effect in both *Polycarpa* and *Polyandrocarpa* species is a limitation of polycarps from a scattered arrangement to two rows parallel to the endostyle. With further reduction in the size of the zooids to the small dimensions of those in colonies of *Symplegma*, *Botryllus*, *Botrylloides*

Kukenthalia and *Chorizocarpa*, a single polycarp is all that can be accommodated on each side of the body. In all of these forms there is further an increase in the size and reduction in number of ova produced by the ovarian component of the polycarp, when compared with a polycarp of species of *Polyandrocarpa*. These genera, accordingly, may form a natural subdivision, or again may merely show converging structure due to a comparable degree of body size reduction.

The gonads in *Polyandrocarpa* are undoubtedly the least modified within the group, with regard to the distribution, number, and nature of each. In *Polyzoa* conditions are similar, except that the units are smaller, both the number of ova and testis follicles being greatly reduced. *Stolonica* has changed little in number and distribution, but the acquisition of a relatively enormous egg size results in the ovary becoming functionally a virtual one-egg ovary, even though other oocytes may be present. The formation of anterior male and posterior hermaphrodite polycarps can be interpreted on the basis of an antero-posterior gradient in the size of the polycarp rudiments at the initiation of their development. In *Metandrocarpa* (s. *Goodsiria*) polycarps are of a single sex, and on both sides there are female gonads with large eggs in the anterior part and male gonads consisting of a single testis in the posterior part (Ritter, 1896); while in *Distomus* (s. *Alloeocarpa*) ovaries with no trace of testis are found in the anterior part of the right side, and testes alone in the posterior part of the left side. Eggs are large and mature singly in both *Metandrocarpa* and *Distomus*.

A comparison of budding has to be less complete since too little is known in some cases, especially concerning the time and localization of the young buds. In general, however, the different genera comprise two groups, one in which budding is essentially a process performed by functional zooids during their later growth phase, and in which buds may grow out from various parts of the posterior and ventral atrial wall; and the other in which there is a small single bud-producing area in the latero-ventral wall.

The interrelations of the various genera therefore are complex and obscure. There has apparently been diverse evolution independently in the three features, branchial structure, nature of gonads, and time and place of budding. Much more detailed information is needed for all but *Botryllus*, *Botrylloides*, *Symplegma* (cf. Berrill, 1940), *Stolonica* and *Distomus*. At the same time *Botryllus*, *Botrylloides*, *Symplegma*, *Kukenthalia* and *Chorizocormus* do have in common the following characters: three inner longitudinal vessels in the branchial sac, a single polycarp on each side, with eggs of a comparable size, and on one side or both budding is confined to a very small area of the lateral wall immediately anterior to the gonad. This may be an instance of parallel evolution, but coincidence of the three features is considerable and it is difficult to avoid the conclusion that at least these five genera form a natural subdivision of the polystyelids.

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STUDIES ON BRITISH LAMINARIACEAE. I. GROWTH IN *LAMINARIA SACCHARINA* (L.) LAMOUR.

By Mary Parke, B.Sc., Ph.D.
Botanist at the Plymouth Laboratory

(Plates V–XIII and Text-figs. 1–10)

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INTRODUCTION

Very little information was available at the beginning of the Second World War on the growth and behaviour of the common British Fucaceae and Laminariaceae when a need for this knowledge arose for economic purposes. An investigation was started, therefore, on these groups at the request of, at first, a private firm, Messrs Cefoil Ltd., and later the Ministry of Supply.

This first paper deals with *Laminaria saccharina* (L.) Lamour. and gives the results of observations made from 1941 to 1945 on the south coast of Devon, in the neighbourhood of Plymouth, and on the coast of Argyll, off the island of Luing. At both places low water of spring tides occurs in the middle of the day and middle of the night.

Most of the literature on the Laminariaceae can be obtained from the references given by Fritsch (1945), but the following Russian papers not included by him give some detailed information on the growth of *L. saccharina* in the northern seas: Kireeva & Schapova (1933, 1938) and Tikhovskaya (1940) deal with the seasonal variation of this species in the Kola Fjord and Barents Sea, working from the size and weight variation of the species throughout the year.

There is no precise information available, however, on the variation in the rate of growth of either the frond or the stipe of individual plants of this species with change in age of the plant and season of the year. Precise information is lacking on the regenerative and propagative powers of this species; also on the variation in the time of production, growth, reproduction, depopulation rate, and longevity of populations growing in different geographical positions, at different bathymetric levels and in different types of habitat.

From the results of the present work some information has been obtained on the above points and, in addition, the results have shown the influence of bathymetric zone and habitat on the behaviour of the gametophyte generation (microscopic) in relation to the time and period of production by it of the sporophyte generation (macroscopic plant).

Many workers, in particular Kjellman (1883), Foslie (1890), Setchell (1900), Børgesen (1903), Killian (1911), Printz (1926), Zinova (1929), Flerov & Karsakoff (1932), have stressed the outward variation in the form of *L. saccharina* plants growing in different types of habitat and have given descriptions, some giving measurements, of the many varieties of this species. Foslie (1890) and Flerov & Karsakoff (1932) have suggested also a possible internal structural variation depending on the latitude at which growth occurs, particular mention being made of the mucilage canal system of the frond.

The variation in the length, width, texture and bullations of the frond, in the shape, length and diameter of the stipe, in the design of the holdfast, and in the size, shape and position of the reproductive tissue on the frond that has been found in this species during the present work can be related to the variation in the rate of growth with changes in age, season, habitat and geographical position (Pls. V–VIII). Not only can growth forms of *L. saccharina* be classed as varieties of the species, some of the forms obtained agree even with the descriptions of distinct species. For instance, second-year plants in very exposed habitats in the intertidal zone agree with Agardh's (1867) description of *L. hieroglyphica*, whilst summer-developed plants at the northern station, in the late spring and summer of the following year, in sheltered habitats in the sublittoral zone, agree with Børgesen's (1903) description of *L. faeroensis*; this species with more rapid stipe growth would resemble *L. longicruris* De la Pylaie of the north-eastern coast of North America if Setchell (1900) is correct in stating that mucilage canals are absent from the stipe.

It would be of great systematic interest if the chromosome numbers were known and transplanting experiments from one latitude to another could be carried out on the following species of *Laminaria*: *L. agardhii* Kjellman, *L. faeroensis* Børgesen, *L. groenlandica* Rosenvinge, *L. longicruris* De la Pylaie, *L. hieroglyphica* J.Ag. and *L. saccharina* (L.) Lamour. Evidence could then be obtained to show whether they are really distinct species or all growth and latitude forms of the one species.

In this work three zones are distinguished on the shore, the intertidal, the sublittoral fringe and the sublittoral.

The *intertidal zone* is regarded as extending from extreme high water of spring tides down to just above low water of mean spring tides.

The *sublittoral fringe zone* is that zone distinguished by Stephenson (1937, 1939) 'to designate the part of the sublittoral zone which extends above extreme low water of spring tides. The fringe remains submerged at low water of neap tides, its degree of emergence at low water of springs depending very much upon variations in wave action.' This zone extends above extreme low water of the lowest spring tides to approximately 0·1 m. above low water of mean spring tides at the southern station and 0·5 m. at the northern station.

The *sublittoral zone* is the region below extreme low water of spring tides in which the attached algae are permanently submerged.

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PRODUCTION OF THE SPOROPHYTE

Schreiber (1930) found that the gametophyte generation of *L. saccharina* growing in culture was perennial but was fertile only during the winter and spring; he attributed the loss of fertility during the summer to the increase in temperature. He found that fertility could be induced during the summer in strains of gametophytes, started during the winter and spring, growing at a temperature of 16–18° C. by lowering the temperature to 6° C. He therefore concluded that there was no inherent seasonal alternation of sterile and fertile periods, but that the power of gamete production was at all times released by the action of suitable external conditions quite independently of the time of the year. As he found young sporophytes in nature only in the spring he believed that, although the gametophyte could be perennial in nature, it was fertile only during the winter months.

The results obtained by Harries (1932) disagree with those of Schreiber, since she states that oogonia develop on female gametophytes in temperatures up to 16° C. She does say, however, that when the temperature is raised above a certain degree it inhibits reproduction although it accelerates growth. She concludes from her experiments that, when there is a suitable light intensity and sufficient phosphate, fertility of the gametophyte varies with the nitrate concentration, but that when there is a sufficient quantity of nitrate and phosphate present in the medium then the fertility varies with the light intensity.

The present investigations have shown that sporophytes of *L. saccharina* can be produced in nature during all months of the year at some level on the shore, on both normal untouched areas and on experimental areas from which the original population had been removed. The gametophyte generation of this species must, therefore, be capable of reproduction during all months of the year.

TABLE I. PRODUCTION OF THE SPOROPHYTE OF *LAMINARIA SACCHARINA* IN RELATION TO BATHYMETRIC ZONE AND HABITAT

Type of habitat	Locality	Names given to experimental areas	Nature of substratum	Observations commenced	Observations ceased	Monthly record of sporophyte production in *L. saccharina* Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	No. of months sporophytes produced in the year
Floating at surface:																		
Permanent submergence at shallow depth at all times	P.	Floating raft	Tarred wood	14. xi. 41	3. viii. 44	×	×	×	×	×	×	×	×	×	×	×	×	12
	A.	Buoys—inner channel	Painted metal	10. i. 42	3. ii. 43	×	×	×	×	×	×	×	×	×	×	×	×	12
Lower intertidal to sublittoral fringe zone:																		
Permanent submergence in pools at M.L.W.S.T.	W.	Inlet—cleared area	Rock	3. iv. 42	1. x. 44	×	×	×	×	×	×	×	×	×	×	×	×	12
	W.	Cloustoni cleared III	,,	26. iii. 44	2. x. 44	.	.	.	×	×	×	×	×	×	.	.	.	
	A.	*Blocks (6)—lobster pond	Concrete blocks on soft mud	20. iv. 42	19. viii. 43	—	—	—	—	—	—	—	—	—	—	—	—	0
Periodical emergence at spring tides	W.	Bay—cleared area	Rock	6. ix. 41	4. x. 44	×	×	×	×	—	—	×	×	×	×	×	×	10
	W.	Digitata cleared I	,,	23. x. 41	4. x. 44	×	×	×	×	?	—	×	×	×	×	×	×	10–11
	W.	Digitata cleared II	,,	10. xi. 42	4. x. 44	×	×	×	×	?	—	×	×	×	×	×	×	10–11
	W.	Digitata cleared III	,,	26. iii. 44	30. ix. 44	.	.	.	.	—	—	×	×	×	.	.	.	
	W.	Cloustoni cleared I	,,	24. ix. 41	2. x. 44	×	×	×	×	?	—	?	×	×	×	×	×	9–11
	W.	Cloustoni cleared II	,,	27. ix. 42	3. x. 44	×	×	×	×	?	—	×	×	×	×	×	×	10–11
	M.	Cloustoni cleared area	,,	22. x. 41	31. x. 44	×	×	×	×	—	—	×	×	×	×	×	×	10
	M.	Digitata cleared area	,,	22. x. 41	31. x. 44	×	×	×	×	—	—	×	×	×	×	×	×	10
	A.	Digitata cleared I	,,	5. xi. 41	5. ix. 44	×	×	×	×	—	—	×	×	×	×	×	×	10
	A.	Digitata cleared II	,,	30. v. 42	4. ix. 44	×	×	×	×	—	—	×	×	×	×	×	×	10
	A.	Cloustoni cleared I	,,	12. ix. 42	4. ix. 44	×	×	×	×	—	—	×	×	×	×	×	×	10
Sublittoral zone:																		
Permanent submergence at depths from 1 to 4 m. below E.L.W.S.T.	A.	Ropes—inner channel, 1 m.	Tarred-manilla	10. i. 42	3. ii. 43	—	?	×	×	×	×	×	×	×	×	—	—	8–9
	A.	Blocks (3) shallow, 1 m.	Concrete on gravel	20. xi. 41	7. ix. 44	—	?	×	×	×	×	×	×	×	×	—	—	8–9
	A.	Blocks (1), 1 m.	,,	16. viii. 43	7. ix. 44	—	—	×	×	×	×	×	×	×	×	—	—	8
	A.	Blocks (6), 2 m.	,,	23. iv. 43	16. viii. 43	.	.	.	.	—	×	×	×	.	.	.	.	
	A.	Blocks (4), 2 m.	,,	26. iv. 44	5. ix. 44	.	.	.	.	—	×	×	—	.	.	.	.	
	A.	Blocks (3) deep, 4 m.	,,	20. xi. 41	3. ii. 43	—	—	—	—	×	×	×	×	×	?	—	—	5–6
	A.	Blocks (6), 1–4 m.	,,	16. viii. 43	5. ix. 44	—	?	×	×	×	×	×	×	×	—	—	—	7–8
	M.	Blocks (6), 4 m.	Concrete on rock	27. iii. 44	20. xi. 45	—	—	—	—	×	×	×	×	×	×	—	—	6
Permanent submergence at depths from 6 to 12 m. below E.L.W.S.T.	A.	Blocks (6), 6–8 m.	Concrete on rock	10. vii. 44	24. ix. 45	—	—	—	—	—	—	—	—	—	—	—	—	0
	A.	Blocks (6), 12 m.	,,	14. viii. 43	9. xii. 43	.	.	.	.	.	.	.	—	—	—	—	—	

× Production of sporophytes during month.
— No production of sporophytes during month.
? Production of sporophytes at the beginning or the end of the month.
* Size of all concrete blocks 0·3 × 0·3 × 0·1 m.; weight of blocks approximately 20 kg.
A. Argyll coast off island of Luing.
M. South Devon coast, Mouthstone Ledges at mouth of River Yealm.
P. South Devon coast, Plymouth Sound.
W. South Devon coast, Wembury, Blackstone Rocks.

External factors, chiefly bathymetric zone and type of habitat, appear to control the fertility and longevity of the gametophyte and consequently the production of the sporophyte. From the observations on normal areas of the shore and on experimental cleared areas (Table I) four groups can be distinguished:

(1) Habitats in which sporophytes are produced during all months of the year.
(2) Habitats in which sporophyte production ceases in the late spring and early summer.
(3) Habitats in which sporophyte production ceases in the winter.
(4) Habitats in which no sporophyte production has been recorded.

Although the sporophytes are produced during these periods it does not necessarily follow that they persist on the shore beyond the sporeling stage.

The first group includes habitats in the intertidal and sublittoral fringe zones that are always covered at low tide, even at extreme low water of spring tides, by up to 0·5 m. of water, that is, intertidal pools. The submerged parts of such objects as floating rafts, buoys, and ropes from just below the surface down to 0·5 m. can also be included in this group. These habitats appear to be the most favourable for the continued production of sporophytes throughout the year. The sporophytes may arise from the persistent fertility of perennial gametophytes or by the development of successive crops of new gametophytes some of which become mature during all months of the year.

The continued production of sporophytes during every month of the year on the floating raft in Plymouth Sound, where the surface water temperature ranges from 7° to 16° C., possibly 17° C., and in the pools on the lower part of the intertidal zone, indicates that actual temperature rise may not be the controlling factor for the fertility of the gametophyte under natural conditions as is suggested by Schreiber (1930).

The results of culture experiments carried out at the Plymouth Laboratory also disagree with Schreiber's results, since gametophytes were fertile from February until May, with the temperature of the cultures rising from 10° to 19° C. When the cultures were discarded in May fertile gametophytes were still present in the cultures.

The second group includes habitats in the intertidal and sublittoral fringe zones that become completely uncovered and dry out during the period of low water of spring tides. The cessation of sporophyte production during May and June in these habitats can be caused by the onset of sterility in the gametophyte or by its complete destruction. Schreiber (1930) found that the gametophytes were killed in a few days if placed near a window in summer light and that at all times the gametophytes were unable to survive drying out, even for a short period. He found that up to a certain extent they were insensitive to a rise in osmotic pressure and that the male gametophytes were more resistant to the rise in osmotic pressure than were the female gametophytes. So strongly developed was this character that the female gametophytes could be completely obliterated from a culture by slow evaporation so that the surviving plants were all male. In these habitats that dry out during low tide it seems more probable that the lack of sporophyte production during May and June is caused by the destruction of the gametophytes, perhaps only the female, during this period rather than by their sterility. This point, however, needs further investigation.

The third group includes habitats in the sublittoral zone 1–4 m. below E.L.W.S.T. The cessation of sporophyte development, possibly gametophyte development also, in these habitats from November to February, is most probably due to the low light intensities reaching these areas during the winter months. Atkins (1939) has shown, expressing the mean monthly daylight values as a percentage of the total for the year, that at Plymouth the lowest figures occur from November to January and that the six months, April to September, receive three-quarters to four-fifths of the annual daylight, an amount which increases with increasing latitude.

The proportion of light reaching the sublittoral experimental areas, compared with the full daylight reaching the floating raft in Plymouth Sound on which sporophytes develop during all months of the year, can be estimated roughly from the figures given by Atkins (1939, p. 148, Table I). Taking the extinction coefficient as 0·40, an approximate value for blue light in turbid inshore waters, then approximately 45% only of the subsurface light is transmitted down to a depth of 1–2 m., and only 14% or less to a depth of 5 m. depending on the turbidity of the water in which a Secchi disc could be seen at rather more than 4 m.

Sauvageau (1918) and Harries (1932) both agree that germination of the gametophyte can occur in the dark, but that a certain intensity of light is necessary for further growth and development. Harries also states that germlings developed in the dark can remain for some months capable of growth on being illuminated.

A fact suggestive also of the influence of the intensity of light is that young sporophytes are rarely found below a thick covering of the fronds of older plants. On some concrete blocks at a depth of 1 m. below E.L.W.S.T., for example, sporophytes, developed in the summer and autumn of 1942 and the spring of 1943, had formed a thick covering over the blocks during the late spring and summer of 1943. No new population developed during the summer of 1943, but in the spring and summer of 1944 sporophyte development restarted on the blocks after the majority of the 1942 and early 1943 populations had gone.

The fourth group includes habitats in the sublittoral zone 6–12 m. below E.L.W.S.T. and also all habitats in all zones where the bottom is of soft mud. Although so far no development of young plants has been obtained on prepared surfaces at depths from 6 to 12 m., well-developed plants of *L. saccharina* have been brought up from depths down to 12 m. These plants, however, were all growing on shingle and may have been washed down into deeper water, having started their development in shallower water.

Habitats with a soft muddy substratum or prepared surfaces placed on soft mud appear to be quite useless for the production of sporophytes. This may be due to the continued sedimentation of the mud either cutting off the light, or smothering any possible gametophyte development, or forming a substratum from which the gametophytes are too easily removed.

Sporophyte production on the British coast can, therefore, be said to take place at the higher levels during the winter, early spring, late summer and autumn, and at the lower levels, down to a certain depth, during spring, summer and early autumn (Table I). In certain specialized types of habitats sporophyte production does not occur, and in others can take place throughout the whole year. In general, this species affords yet another example of algal migration up and down the shore first mentioned by Knight & Parke (1931), and since noted by other workers.

LONGEVITY AND RATE OF DEPOPULATION OF THE SPOROPHYTE

Throughout the period of sporophyte production at all levels and in all habitats a proportion, usually high, of the sporelings become detached from the substratum when they reach a length of from 1 to 2 cm. The variation in numbers of sporelings lost during the first month of growth and the longevity of the plants which survive the sporeling stage appear to be dependent on two factors, the time of the year at which germination of the plant occurs and the type of habitat in which it arises.

The data on the longevity and rate of depopulation of this species, taken from the records of populations that developed on experimental areas from 1941 to 1945, is summarized under three headings according to the time of germination of the sporophytes. Table II records the maximum ages, in months, reached by populations growing under different habitat conditions on the experimental areas.

Sporophytes arising in the Winter (November to February)

Winter sporophytes, produced only in the intertidal and sublittoral fringe zones, rarely survive beyond the sporeling stage unless the habitat is one of extreme shelter. The figures show that the loss of winter sporophytes during the first month of growth ranges from a 95% loss in sheltered habitats to a 100% loss in exposed habitats. The complete removal of winter sporophytes during the first month of growth takes place consistently year after year in all habitats with any degree of exposure, irrespective of whether the habitat dries out or remains covered by a shallow depth of water at low tide (Table II, nos. 2–6).

TABLE II. LONGEVITY OF THE SPOROPHYTE OF *LAMINARIA SACCHARINA* IN RELATION TO TIME OF GERMINATION, BATHYMETRIC ZONE AND HABITAT

Type of habitat	Locality	Names given to experimental areas	Nature of substratum	Observations commenced	Observations ceased		Maximum age in months of *L. saccharina* shown against dates of germination											
							Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Floating at surface:																		
Permanent submergence at shallow depth at all times	P.	(1) Floating raft	Tarred wood	14. xi. 41	30. x. 43	1941:	—	—	—	—	—	—	—	—	—	—	—	23+*
						1942:	22+	21+	20+	19+	18+	17+	16+	15+	14+	13+	12+	11+
						1943:	10+	9+	8+	7+	6+	5+	4+	3+	2+	1+	—	—
Lower intertidal to sublittoral fringe zone:																		
Permanent submergence in pools at M.L.W.S.T.	W.	(2) Inlet-cleared area	Rock	3. iv. 42	26. vi. 45	1942:	—	—	—	23	22	21	8	7	6	5	<1	<1
						1943:	<1	<1	<1	26+	25+	20	7	6	5	4	<1	<1
						1944:	<1	<1	16+	15+	14+	8	7	6	5	—	—	—
Periodical emergence at spring tides	W.	(3) Digitata cleared I	Rock	23. x. 41	4. x. 44	1941:	—	—	—	—	—	—	—	—	—	—	<1	<1
						1942:	<1	<1	26	25	—	—	8	7	6	5	<1	<1
						1943:	<1	<1	19+	18+	—	—	7	6	5	4	<1	<1
						1944:	<1	<1	7+	6+	—	—	3+	2+	1+	—	—	—
Do.	W.	(4) Digitata cleared II	Rock	10. xi. 42	4. x. 44	1942:	—	—	—	—	—	—	—	—	—	—	<1	<1
						1943:	<1	<1	<1	18	—	—	7	6	5	4	<1	<1
						1944:	<1	<1	<1	6+	—	—	3+	2+	1+	—	—	—
Do.	A.	(5) Digitata cleared I	Rock	5. xi. 41	5. ix. 44	1941:	—	—	—	—	—	—	—	—	—	—	—	<1
						1942:	<1	<1	18	17	—	—	11	10	9	8	<1	<1
						1943:	<1	<1	8	7	—	—	3	2	—	—	—	—
Do.	A.	(6) Digitata cleared II	Rock	30. v. 42	4. ix. 44	1942:	—	—	—	—	—	—	11	10	9	8	<1	<1
						1943:	<1	<1	12	11	—	—	8	7	6	5	<1	<1
Sublittoral zone:																		
Permanent submergence at 1 m. depth below E.L.W.S.T.	A.	(7) Blocks (3) shallow	Concrete on gravel	20. xi. 41	7. ix. 44	1942:	—	—	—	—	—	—	27+	26+	25+	24+	—	—
						1943:	—	—	19+	18+	—	—	—	—	—	—	—	—
						1944:	—	—	7+	6+	5+	4+	3+	2+	1+	—	—	—

* + sign after a figure denotes that population still represented when observations ceased.
A. Argyll coast off island of Luing.
P. South Devon coast, Plymouth Sound.
W. South Devon coast, Wembury, Blackstone Rocks.

On three experimental areas only did winter sporophytes survive beyond the sporeling stage (Table II, no. 1). These were the 'Lobster Pond' off the west coast of the island of Luing, an artificial pond situated between small islands, the 'floating raft' anchored just inside and protected by the Breakwater in Plymouth Sound, and the sublittoral fringe zone on the north side (protected) of the Plymouth Breakwater.

On substrata, other than rock, for example, gravel mixed with small stones as found in the 'Lobster Pond', the winter sporophytes which survive the sporeling stage disappear from the shore during the first few months of growth. They may be washed down into deeper water where they survive to maturity, but this has not been proved.

Although winter sporophytes growing on the 'floating raft' had to be removed when up to 23 months old, as the raft was required for other purposes, labelled plants on the north side of the Breakwater showed that very small numbers of winter sporophytes survived into the third year of growth. These sporophytes disappeared from the shore during the fourth winter when the plants were approximately 3 years old.

As the development of winter sporophytes has not been recorded for the sublittoral zone, except perhaps during late February, the only type of natural habitat in which winter sporophytes are known to persist to maturity is one with a rocky substratum in the intertidal or sublittoral fringe zones on coasts where there is extreme shelter.

SPOROPHYTES ARISING IN THE SPRING (MARCH TO MAY)

During the spring months sporophyte production occurs in the sublittoral zone in addition to the intertidal and sublittoral fringe zones, and therefore takes place over a more extended range during the spring than during the winter. Greater numbers of sporelings also are produced during the spring than during the winter in the intertidal and sublittoral fringe zones, except during May in habitats that dry out at low tide. Winter counts of sporelings give up to 2500 developing on 1 m.^{2}, whilst spring counts of the sporelings give up to 5300.

Not only is there a larger production area and a much greater fertility of the gametophytes at all levels during the spring than during the winter, but there is also a higher percentage survival rate of the sporeling stage at all levels in both sheltered and exposed habitats. The higher survival rate of spring sporelings is due, most probably, to the more rapid initial growth of the spring plants. As the initial growth is more rapid, holdfast development is also more rapid and consequently a firm attachment to the substratum is procured more quickly in the spring than in the winter.

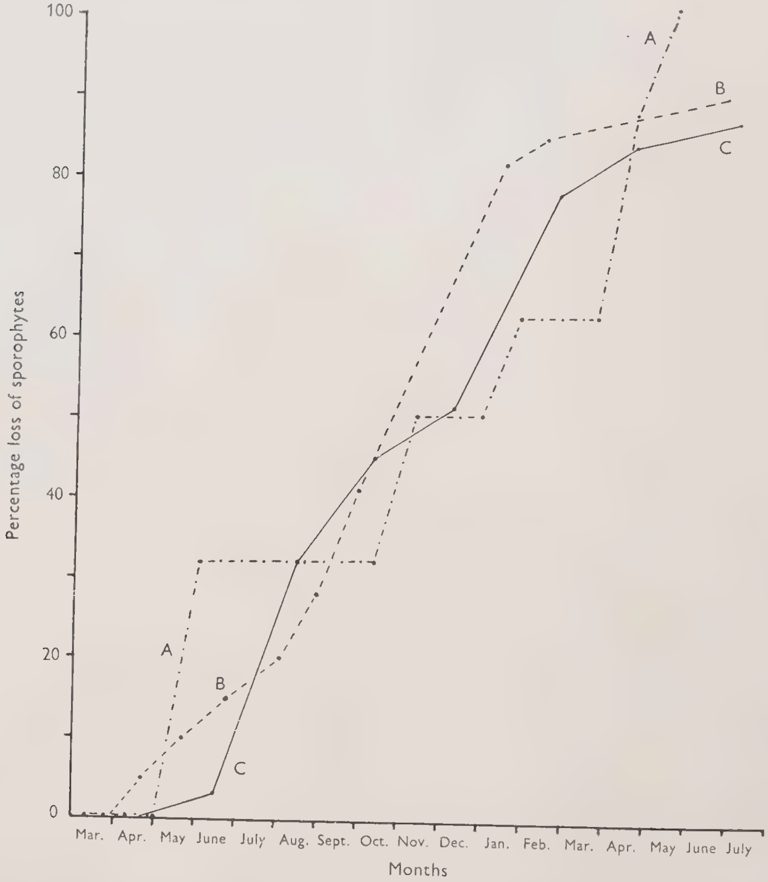
In very sheltered habitats in the intertidal and sublittoral fringe zones the rate of depopulation of spring sporophytes is approximately the same as in the sublittoral zone on the less exposed parts of the coast. In these habitats from

40 to 50% of the sporelings go from the substratum during the first 2 months of growth; a further 15–20% are lost from the second to the fourth month and another 5–10% from the fourth to the sixth month. Thus, by the time a population, growing under sheltered conditions, has reached 6 months old, 60–80% of the original population has been detached from the substratum. Loss in numbers continues throughout the life of a population, at 12 months old from 86 to 91% has been lost and at 24 months old from 98 to 99%. At the end of 2 years, therefore, there is not more than 2% of the original population left on the shore to continue growth in the third year. Spring populations in the third year of growth can survive through the third summer, but they disappear during the third winter when the populations are nearly 3 years old.

On an exposed coast at all levels the rate of depopulation of the sporelings and of the young plants is more rapid. In habitats where there is any degree of exposure, from 60 to 65% of the sporelings become detached during the first 2 months of growth, a further 18–20% during the third and fourth months and another 7–10% during the fifth and sixth months. On an exposed coast, therefore, a population 6 months old has lost from 85 to 95% of its original number, a loss which is 15–25% higher than on a more sheltered coast. By the twelfth month 94–97% of the population has gone, and during the next 12 months the remainder of the population may go in some habitats, but in others up to 0·7% may persist into the third year of growth. It is generally on intertidal and sublittoral fringe zone areas which dry out at low water of mean spring tides that plants do not survive beyond an age of 2 years (Table II, no. 3). In the sublittoral zone and in pools in the intertidal and sublittoral fringe zones the small percentage of a population that has survived up to 2 years, can live on through the third summer (Table II, no. 2), but goes from the substratum during the third winter when the population is nearly 3 years old.

The figures given above indicate that in all spring-developed populations of *L. saccharina* the largest number of plants, 86–97% of a population, become detached during the first year of growth. During the second year, however, the figures for the depopulation-rate of labelled plants shows that the heaviest losses of plants occur at different times of the year at different levels and in different types of habitats (Text-fig. 1). In the intertidal and sublittoral fringe zone areas that dry out at low tide, although there is fairly heavy loss during the autumn and early winter months, the heaviest loss takes place during the spring—in May at the beginning of the second year, and during April and May at the beginning of the third year when all surviving plants succumb.

At the same levels, but in habitats which remain submerged at a shallow depth at low tide, there is some loss during the spring and the summer months; but the heaviest loss of second-year plants occurs during the autumn and early winter months (Text-fig. 1 B). In the sublittoral zone, even on sheltered coasts, heavy losses occur at two seasons of the year, during the summer from June to August and during the winter from December to February (Text-fig. 1 c).

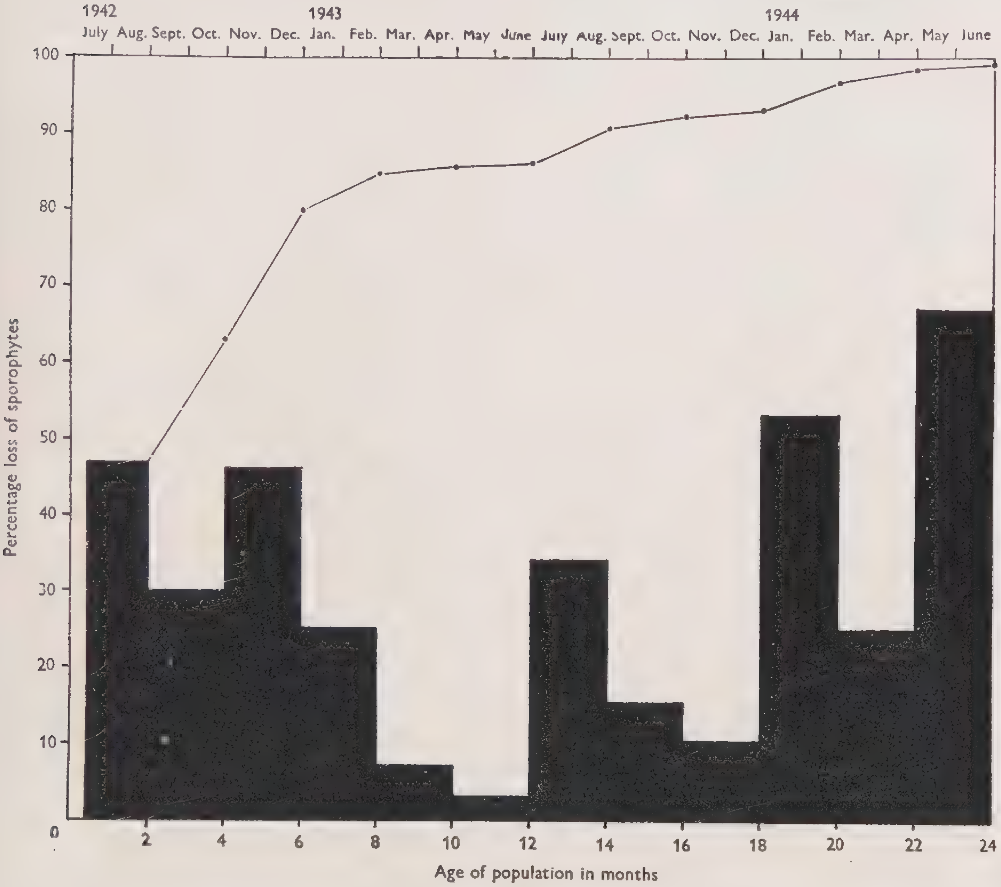


Text-fig. 1. Depopulation in three spring populations of *L. saccharina*, growing in different habitats, from the 13th to 27th month of life. A, exposed shore, intertidal zone, above M.L.W.S.T. B, exposed shore, intertidal zone, at same level as above, but submerged in pools. C, sheltered shore, sublittoral zone, at a depth of 1 m. below E.L.W.S.T.

Spring sporophytes in all habitats, except perhaps in the sublittoral zone on very sheltered coasts, can be said to form, at all times of the year, the bulk of any *L. saccharina* population occurring on the shore, since they are more persistent in nearly all habitats than either the summer or the winter sporelings.

SPOROPHYTES ARISING IN THE SUMMER AND AUTUMN (JUNE TO OCTOBER)

The longevity of sporophytes produced during the summer and autumn is controlled mainly by the nature of the habitat in which development occurs. At all levels, on shores with any degree of exposure, summer and autumn sporophytes rarely survive beyond the first winter although equally large numbers are produced as during the spring (Table II, nos. 2, 3, 4). Spring sporophytes by October are more robust and more firmly attached to the substratum than are the summer and autumn sporophytes and consequently stand a better chance of survival during the winter months than do the later developed plants.



Text-fig. 2. Depopulation during the first 2 years of growth in a summer-developed population of *L. saccharina*, growing on a sheltered shore in the sublittoral zone at a depth of 1 m. below E.L.W.S.T. The upper curve gives progressive percentage loss throughout the 2-year period. Solid columns give percentage loss of the population present 2 months earlier.

The very small numbers of summer and autumn sporophytes that may survive the first winter in habitats which dry out at low tide disappear from the shore during the early part of the following summer before maturity has been reached (Table II, nos. 5, 6). The only summer sporophytes that may survive, in any number, into the second year in exposed habitats are those developed either in the sublittoral zone or on areas which remain covered by a shallow depth of water at low tide (Table II, no. 2). In these habitats, since no cessation of sporophyte production occurs during June, early summer sporophytes may survive their first winter since, as spring plants, they are strongly attached to the substratum before the onset of winter. These plants may live through the second summer but they usually go from the shore during the second winter at an age of about 1½ years.

In very sheltered habitats in the intertidal and sublittoral fringe zones, particularly where there is a rocky substratum, summer and autumn sporophytes may survive the first winter and the second summer, but the majority become detached during the second winter when the plants are about 1½ years old. Only a very small percentage survive the second winter and these go from the shore during the following summer or winter when the plants are from 2 to 2½ years old.

On coasts with a fair degree of shelter the summer and autumn sporophytes of the sublittoral zone survive the first winter equally as well as do the spring sporophytes (Table II, no. 7; Text-fig. 2). At 1 year old 86% of a summer population has gone from the substratum, and at 2 years old 99·2% of the original population, a figure only slightly higher than for a spring population. The small percentage, 0·8%, that lives through the third summer disappears during the third winter at an age of about 2½ years. As in spring sporophytes developed in the sublittoral zone, the heaviest losses in numbers of summer sporophytes, after the first year of growth, occur during two periods of the year, late spring-summer and winter (Text-fig. 2).

There is no indication from the normal populations of *L. saccharina* examined that any plants reach the fourth year of growth, even plants unattached in the sublittoral zone. From the foregoing data it is suggested that the life-span of the sporophyte of *L. saccharina*, on the coasts of Britain, does not exceed 3 years. A study of holdfast, stipe and frond development in first-, second- and third-year plants, the results of which are dealt with in detail in the next section, shows that in this species the peak of growth occurs in the second year of life, thus indicating the short-lived nature of the species.

The information that has been obtained during this work makes it possible to give an indication as to the composition of *L. saccharina* populations in year classes at different levels and in different habitats on the shore during each season of the year. This estimation is given in Table III. The knowledge of the components of a 'normal' population of *L. saccharina* growing in any particular habitat is of importance since from it the approximate extent of the reproductive period of that population can be estimated.

TABLE III. THE COMPOSITION OF *LAMINARIA SACCHARINA* POPULATIONS IN YEAR CLASSES AT DIFFERENT LEVELS AND IN DIFFERENT HABITATS DURING EACH SEASON OF THE YEAR

Season of the year	Winter				Spring				Summer				Autumn			
Time of year populations were produced ...	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Nature of habitat:																
Exposed coast, intertidal and sublittoral fringe zones; emergence at spring tides	1st†*	1st	1st	1st	—	1st†	1st	1st	—	1st	1st†	1st*	—	1st	1st	1st†
	—	2nd	—	—	—	2nd	—	—	—	2nd	2nd*	—	—	2nd	—	—
	—	—	—	—	—	3rd*	—	—	—	—	—	—	—	—	—	—
Exposed coast, intertidal and sublittoral fringe zones, in pools	1st†*	1st	1st	1st	—	1st†	1st	1st	—	1st	1st†	1st*	—	1st	1st	1st†
	—	2nd	2nd*	—	—	2nd	—	—	—	2nd	2nd	—	—	2nd	2nd	—
	—	3rd*	—	—	—	3rd	—	—	—	3rd	—	—	—	3rd	—	—
Exposed coast, sublittoral zone, 1–4 m. below E.L.W.S.T.	—	1st	1st	1st	—	1st†	1st	1st	—	1st	1st†	1st	—	1st	1st	1st†
	—	2nd	2nd*	2nd*	—	2nd	—	—	—	2nd	2nd	—	—	2nd	2nd	2nd
	—	3rd*	—	—	—	3rd	—	—	—	3rd	—	—	—	3rd	—	—
Sheltered coast, intertidal and sublittoral fringe zones; emergence at spring tides, or in pools	1st†	1st	1st	1st	1st	1st†	1st	1st	1st	1st	1st†	1st	1st	1st	1st	1st†
	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd
	3rd	3rd*	3rd*	3rd*	3rd	3rd	—	—	3rd	3rd	3rd	—	3rd	3rd	3rd	3rd
	4th*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sheltered coast, sublittoral zone, 1–4 m. below E.L.W.S.T.	—	1st	1st	1st	—	1st†	1st	1st	—	1st	1st†	1st	—	1st	1st	1st†
	—	2nd	2nd	2nd	—	2nd	2nd	2nd	—	2nd	2nd	2nd	—	2nd	2nd	2nd
	—	3rd*	3rd*	3rd*	—	3rd	—	—	—	3rd	3rd	—	—	3rd	3rd	3rd

† Sporeling stages.

* Maximum age reached by population. For example, winter sporophytes germinate in the 1st winter, second year growth starts in the 2nd winter, third year growth starts in the 3rd winter and the plants become detached during the 4th winter when approximately 3 years old. The winter populations are the only populations to survive a full 3 years; spring sporophytes can survive 2¾ years, summer sporophytes 2½ years and autumn sporophytes 2¼ years.

GROWTH OF THE SPOROPHYTE

Although the sporophyte of *L. saccharina* shows continuous growth throughout its life, very considerable variation occurs in the rate of the growth in both the frond and the stipe during the different seasons of the year. The change in the rate of growth with the time of the year produces periods of rapid and slow growth which alternate during the life of the sporophyte. As the rate of growth of the sporophyte rises gradually to a maximum and then drops gradually to a minimum during each yearly cycle two growth periods, one 'rapid' and one 'slow', are distinguished in each yearly cycle in the development of this species. The 'period of rapid growth' starts in January and continues until June-July with the most rapid growth taking place from March to June, whilst the 'period of slow growth' is from July to December with the slowest growth occurring between September and December.

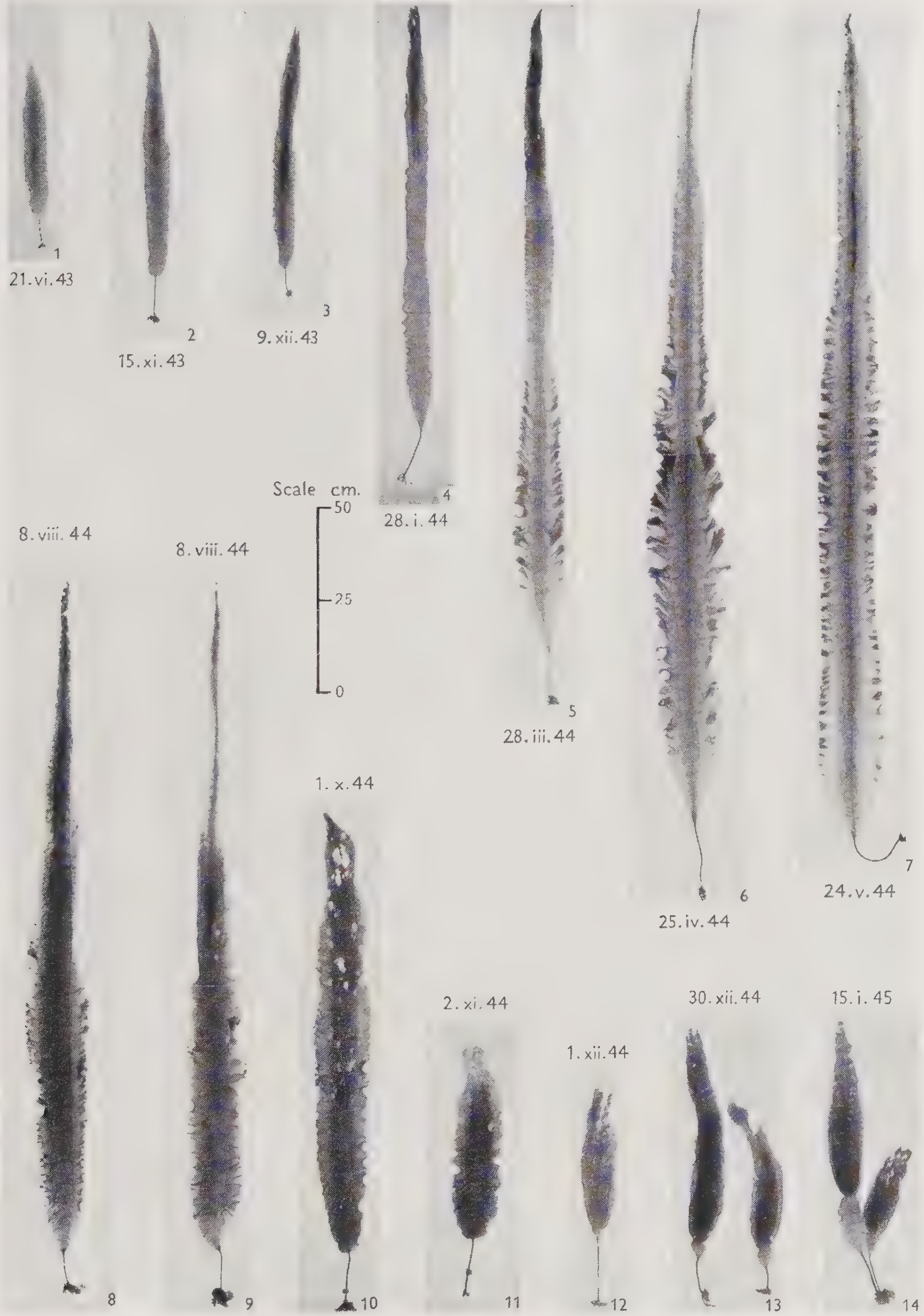
The sporelings show variation also in the rate of development with the time of the year at which they arise, developing very much more rapidly during the rapid-growth period of the older plants than during the slow-growth period. For instance, sporophytes developing on experimental areas at Wembury reached 20 cm. in length in 4 weeks when they arose during the months of April and May, but when development started in November the sporelings grew very slowly, reaching a length of only 2 cm. in 4 weeks. Similar results were obtained in cultures set up in the laboratory at Plymouth. Here zygotes of *L. saccharina*, developing during the months of November and December, took 6 weeks to produce sporophytes with a length of from 2 to 3 cm. At this stage complete differentiation into stipe and frond had been attained and the first row of true haptera had been formed and was attached.

PLATE V. *Laminaria saccharina* (L.) Lamour.

Photographs of different-aged plants from a population that arose in April 1943 on a cleared experimental area on the Blackstone Rocks, Wembury, Devon. Fairly exposed habitat in the intertidal zone (0·2 m. above M.L.W.S.T.) with shallow submergence at low water of mean spring tides. $\times \frac{1}{20}$.

Fig. 1. Three-months-old plant—sterile. 21. vi. 1943.
Fig. 2. Seven-months-old plant—immature reproductive tissue. 15. xi. 1943.
Fig. 3. Eight-months-old plant—mature reproductive tissue: first sporulation. 9. xii. 1943.
Fig. 4. Ten-months-old plant—mature reproductive tissue. 28. i. 1944.
Fig. 5. Twelve-months-old plant—liberation of zoospores practically ceased. 28. iii. 1944.
Fig. 6. Thirteen-months-old plant—sterile. 25. iv. 1944.
Fig. 7. Fourteen-months-old plant—sterile. 24. v. 1944.
Fig. 8. Sixteen-months-old plant—immature reproductive tissue. 8. viii. 1944.
Fig. 9. Sixteen-months-old plant—mature reproductive tissue. 8. viii. 1944.
Fig. 10. Eighteen-months-old plant—mature reproductive tissue. 1. x. 1944.
Fig. 11. Nineteen-months-old plant—mature reproductive tissue. 2. xi. 1944.
Fig. 12. Twenty-months-old plant—mature reproductive tissue. 1. xii. 1944.
Fig. 13. Twenty-one-months-old plant—mature reproductive tissue. 30. xii. 1944.
Fig. 14. Twenty-two-months-old plant—mature reproductive tissue. 15. i. 1945.

PLATE V


1
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28.i.44
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2.xi.44
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12
30.xii.44
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15.i.45
14

Figs. 1–14.

In the frond the change in the rate of the growth throughout a yearly cycle is indicated by the change in the shape of the base and also by the variation in the width of the tissue produced during the different seasons (Pls. V–VII, IX–XI). As tissue is cast off from the distal end of the frond normally when it reaches the age of 6 or 7 months (Pls. IX–XI), a population must be examined at intervals throughout a complete year if the change in frond width is to be followed.

The periods of varying rate of growth can be seen reflected most clearly, however, in the perennial part of the sporophyte, in the alternate light and dark 'ring' formation (Pl. XIII) that shows in the stipe and holdfast, the darker 'rings' being formed by the tissue developed during the periods of slower growth.

GROWTH OF THE FROND

The growth in length of the frond, the variation in the frond width and the loss of distal (apical) frond tissue have been followed in *L. saccharina* plants (sporophytes), developing under different habitat conditions on the shore, from the earliest visible stages up to the age of approximately 2 years.

Pls. IX–XI have been compiled from the records of plants of known age growing on experimental areas. Pl. IX covers the period from March 1942, when the plants were first visible on the shore, to April 1944, the month in which the last record was taken before the plants disappeared. This diagram illustrates the behaviour of frond tissue on plants, growing intertidally on an exposed shore, in habitats which are uncovered when low water is at the level of mean springs.

For the sake of contrast to the above, plants were studied growing at the same level on the same shore, but remaining permanently submerged in pools. Pl. X illustrates the growth of such plants, covering a period of 2 years and 3 months from April 1943, when the plants germinated.

In Pl. XI growth of the frond of summer-developed plants in the upper part of the sublittoral zone (1 m. below E.L.W.S.T.) is illustrated, and covers also a period of 2 years from July 1942 to July 1944.

In the diagrams on Pls. IX–XI the thick line running through and across the columns joins up the average actual frond length of the population at the times of measurement, the length of the column above this line indicating the average amount of frond length that has been cast off by the population up to that date since the time of germination. The thin line joining up the tops of the columns gives the curve for the overall growth in length of the frond, including the cast-off tissue.

The solid block at the base of each of the columns shows the average length of frond added by the population since the previous measurement, whilst the hatched part of the column, immediately above the thick line denoting frond length, gives the average amount of frond tissue that has been cast off by the population since the previous measurement.

In the final column of each of the three diagrams are shown: (i) the total average frond length that has been produced by a plant of each of the populations during the complete period of observation, and (ii) the variation in the average width of the frond, at the same scale as frond length, throughout the whole period. On the left side of these final columns the average monthly growth in the length of the frond is marked off, and on the right side of the columns is recorded the approximate period during which each month's frond tissue is cast.

Growth in Length

General Rhythm in Rate of Growth

The general rhythm in the rise and fall in the rate of growth in length of the frond during a yearly cycle in any *L. saccharina* population can be seen from an examination of Pls. IX–XI and Text-fig. 3. These figures show that in general, whatever the age, habitat, latitude or time of germination of the population, frond growth in length is at a more rapid rate from January to June-July than from July-August to December. They show also that during the period of more rapid growth, January to June, the rate of growth gradually increases from January until March, the rate then either still increasing or remaining fairly stable during the period of the most rapid growth from March to May-June.

Towards the end of the period of rapid growth the rate begins to slow down, gradually decreasing from June-July onwards during the period of slower growth, July to December, until the minimum rate is reached during the months of either October or November, after which the rate again begins to rise.

PLATES VI and VII. *Laminaria saccharina* (L.) Lamour.

With the exception of Figs. 15 and 20 the photographs are of different-aged plants from a population that arose in July 1942 on experimental blocks situated off the west coast of the island of Luing, Argyll. Blocks at 1 m. depth below E.L.W.S.T. in a sheltered habitat. The plant illustrated in Fig. 20 is a second-year plant growing in the same habitat but from a different experimental series. 'Four-holed punch' indicates that four holes were punched in the frond of a plant at 2·5, 5·0, 7·5 and 10·0 cm. above the base. $\times \frac{1}{20}$.

PLATE VI

Fig. 15. Plants less than 2 months old growing on the stipe of an older plant.

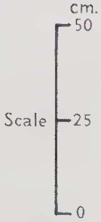
Fig. 16. Plants 3–4 months old—sterile.

Fig. 17. Plants up to 6 months old growing on one of the concrete blocks—sterile.

Fig. 18. Ten-months-old plant—sterile. 22. iv. 1943. A, single-hole punch 2·5 cm. above the base, 12. xi. 1942; B–C, four-holed punch, 6. ii. 1943.

Fig. 19. Twelve-months-old plant—first development of reproductive tissue (immature). 21. vi. 1943. A–B, four-holed punch, 22. iv. 1943. This plant was one of the largest 1-year-old plants on the experimental blocks; it weighed 1·928 kg. ($4\frac{1}{4}$ lb.).

15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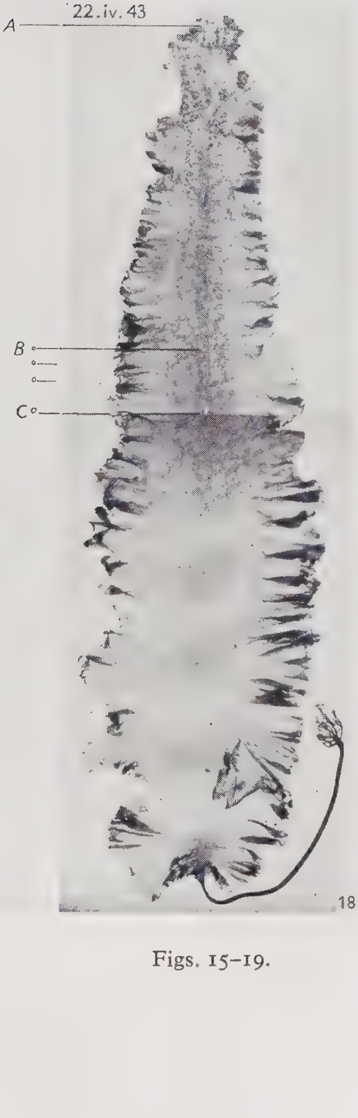

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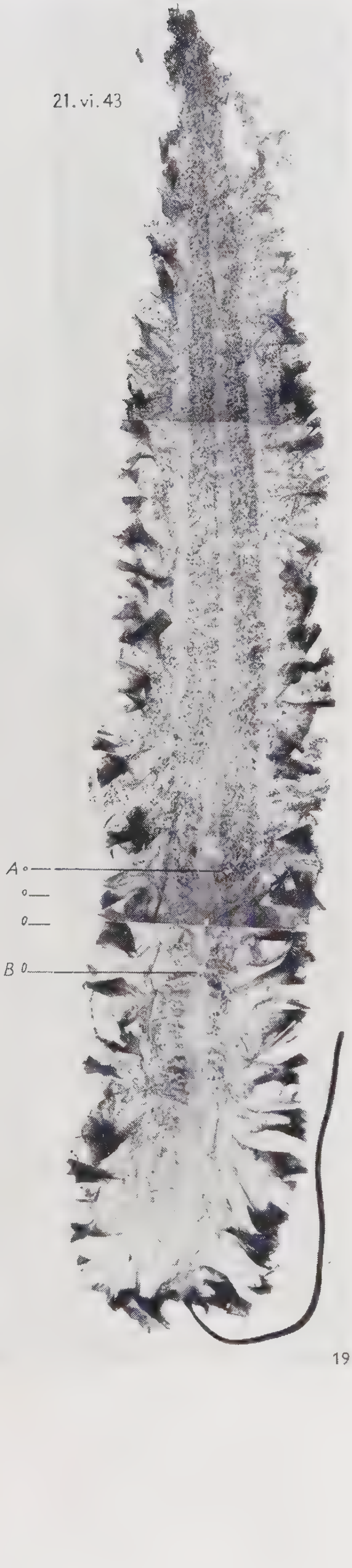

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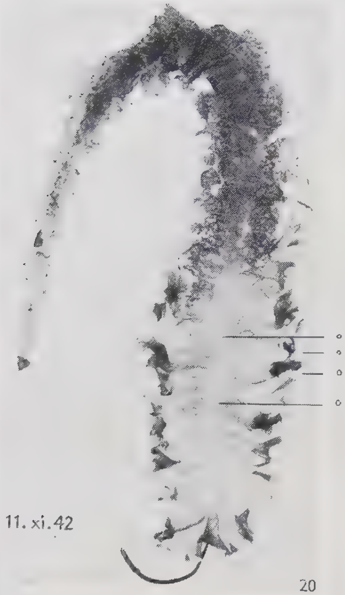
Figs. 15–19.



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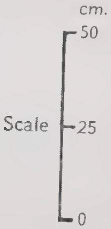
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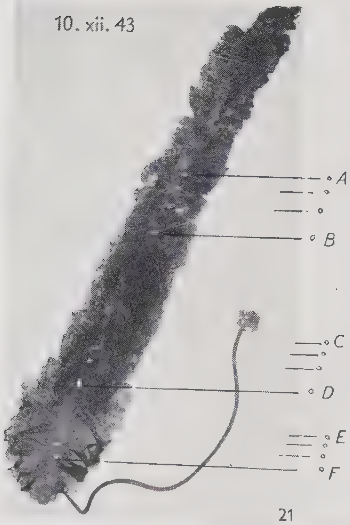
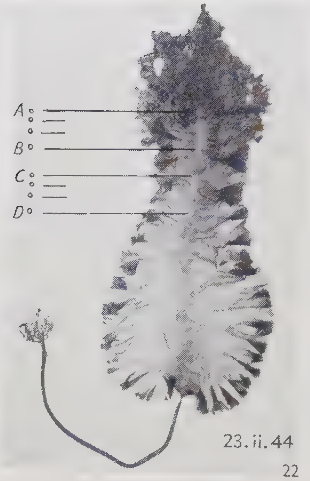

10. xii. 43
A
B
C
D
E
F

21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B
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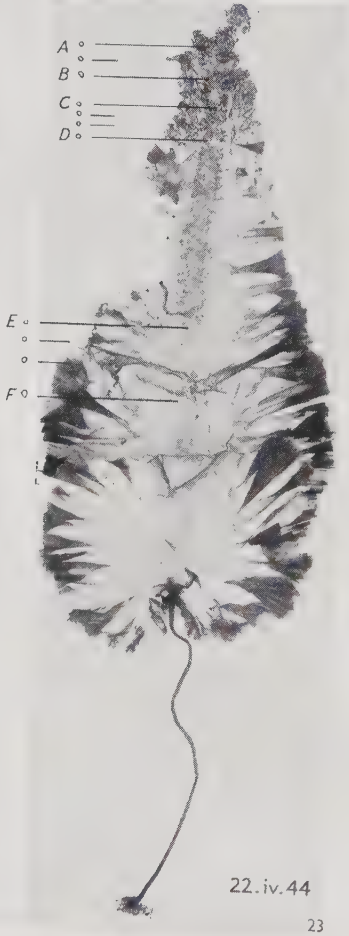
23. ii. 44

22


A
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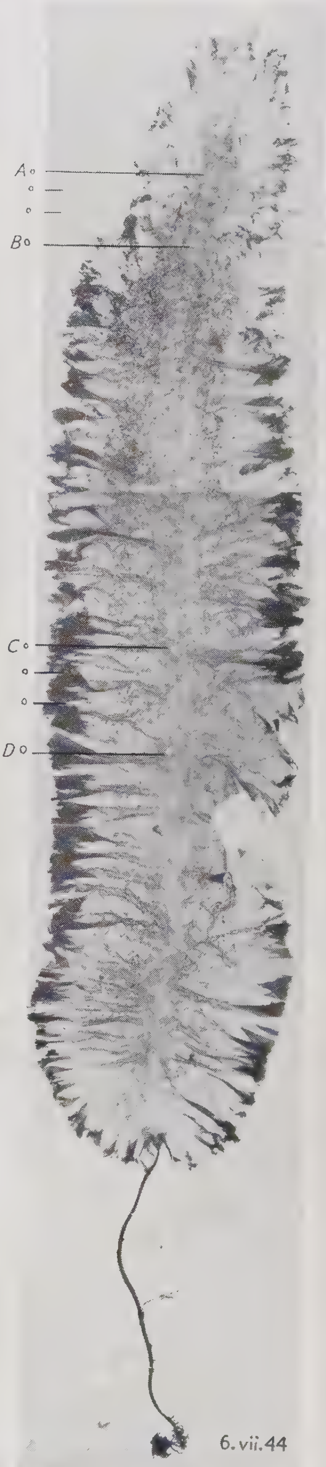
22. iv. 44

23


A
B
C
D
6. vii. 44

24

Figs. 20–24.

Variation in Rate of Growth

For the variation in the rate of frond growth in length that occurs among the plants of this species, irrespective of the general rhythm in growth-rate that takes place during a yearly cycle, the following factors appear to be responsible: (i) age and season of development of the plant, (ii) habitat, and (iii) geographical position.

In Text-fig. 3, graphs 1–6 illustrate the average daily growth in frond length for six populations of *L. saccharina* growing in different types of habitat on the Devon and Argyll coast, and cover periods of from 7 to 27 months. Graphs 1, 4 and 6 of this figure give the daily growth in frond length of the three populations illustrated in detail in Pls. IX–XI. The figures given in these graphs can be approximate only, since the average daily growth figure for the period between measurements makes no allowance for any alteration in the rate of growth within any one period. These figures are reproduced as they demonstrate to some extent, first, the change in the rate of frond growth in length throughout the year and the rapidity with which it is possible for frond tissue to be produced (nos. 5, 6); secondly, the change in the rate of growth with the increase in the age of the population (nos. 1, 4, 5 and 6) and the difference in rate of growth of populations arising at different times of the year (nos. 5, 6); thirdly, the variation in rate of growth with the type of habitat (nos. 1, 4 and 5); and fourthly, the variation in the growth-rate with change in geographical position (nos. 2, 3).

The influence of the *age of the plant* on the rate of growth in length of the frond can be traced in Pls. IX–XI; Text-fig. 3, nos. 1, 4, 5 and 6. The sequence of this variation in rate of growth with increase in age can be seen more clearly when the rate of growth is traced through the successive growth periods in the life of the plant—first, second and third rapid- and slow-growth periods, rather than when followed through yearly cycles starting with the month of germination of the plant.

When growth is traced in the former way the figures show that the rate of frond development in length during the first rapid-growth period is not so

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PLATE VII

Fig. 20. Sixteen-months-old plant—mature reproductive tissue. 11. xi. 1942. A–B, four-holed punch, 16. ix. 1942.

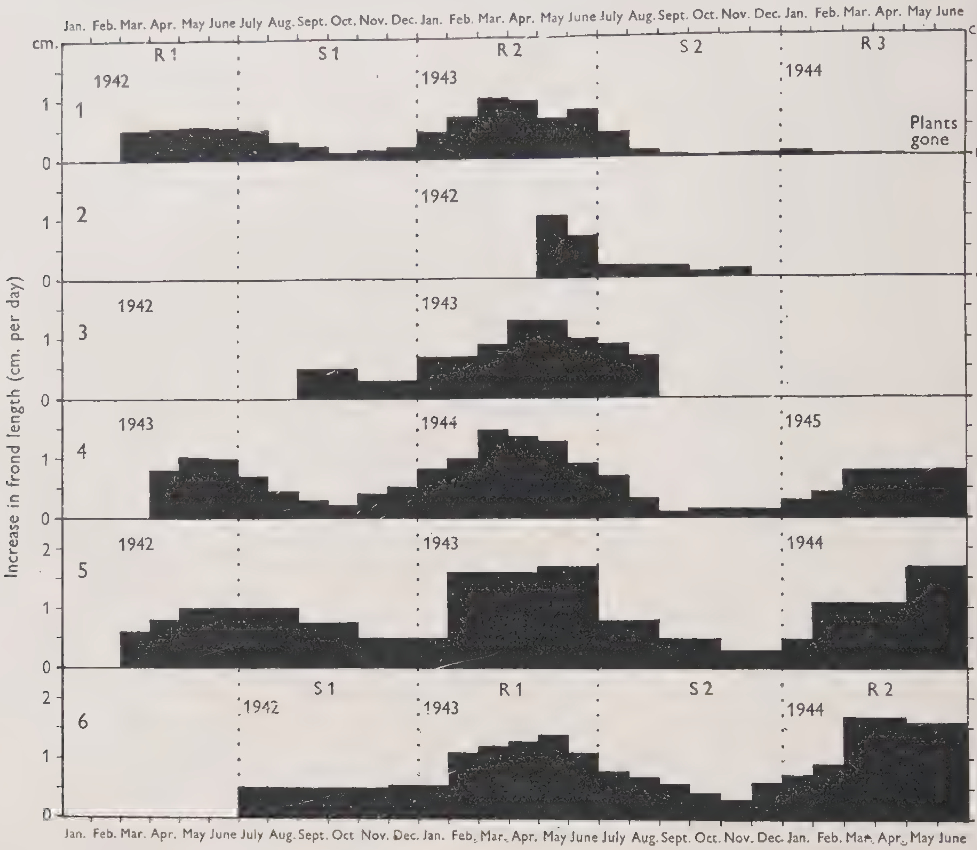
Fig. 21. Eighteen-months-old plant—mature reproductive tissue. 10. xii. 1943. A–B, four-holed punch, 16. vi. 1943; C–D, four-holed punch, 16. viii. 1943; E–F, four-holed punch, 13. x. 1943.

Fig. 22. Twenty-months-old plant—mature reproductive tissue. 23. ii. 1944. A–B, four-holed punch, 13. x. 1943; C–D, four-holed punch, 10. xii. 1943.

Fig. 23. Twenty-two-months-old plant—sterile. 22. iv. 1944. A–B, four-holed punch, 13. x. 1943 (three holes remain); C–D, four-holed punch, 10. xii. 1943; E–F, four-holed punch, 23. ii. 1944.

Fig. 24. Twenty-four-months-old plant—immature reproductive tissue. 6. vii. 1944. A–B, four-holed punch, 23. ii. 1944.; C–D, four-holed punch, 22. iv. 1944.

great as during the second rapid-growth period, and that the rate reached during the third period never surpasses that achieved during the second period.



Text-fig. 3. Daily growth in frond length in six populations of *L. saccharina*, showing the variation in growth-rate with age, season, habitat and locality.

(1) Spring population, March 1942. Devon, exposed shore, intertidal zone, above M.L.W.S.T. (thus periodically uncovered).

(2) Normal population. Devon, very sheltered shore, intertidal zone, above M.L.W.S.T.

(3) Normal population. Argyll, very sheltered shore, intertidal zone, above M.L.W.S.T.

(4) Spring population, April 1943. Devon, exposed shore, intertidal zone (above M.L.W.S.T.), in pools (thus never uncovered).

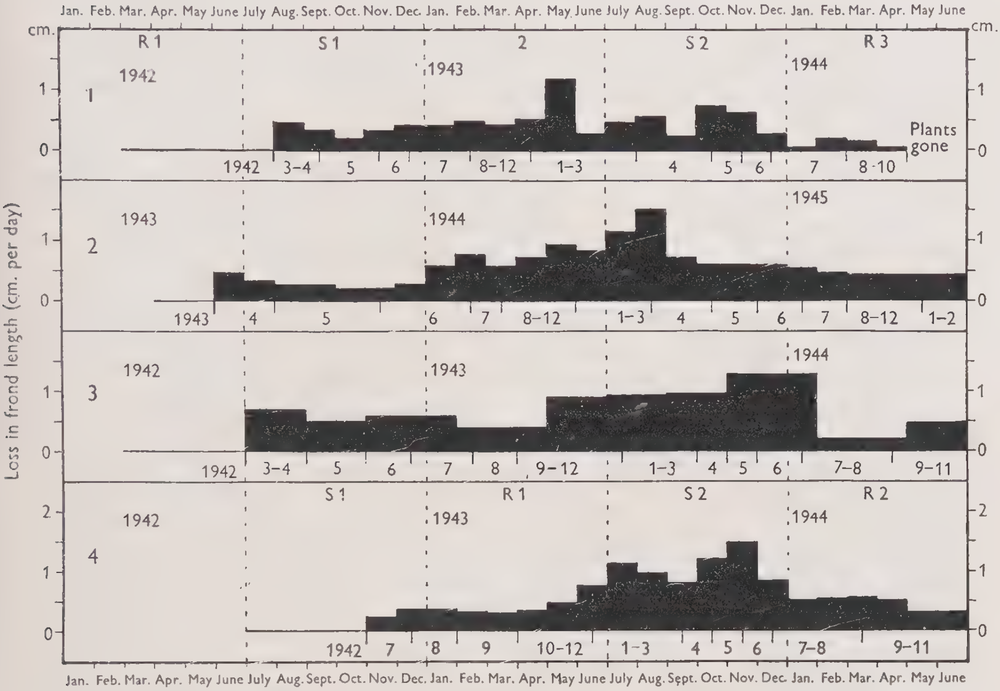
(5) Spring population, March 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

(6) Summer population, July 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

R, rapid-growth period. S, slow-growth period.

The variability in the rate of frond growth during the third rapid-growth period, when compared with the growth during the second rapid-growth period in the same habitat, is so pronounced among populations growing in different habitats that factors external to the plant appear responsible and will be discussed later (compare Pls. IX, X; Text-fig. 3, nos. 1, 4 and 5).

During the slow-growth periods, however, the rate does not slow down to the same degree, nor does the slowest rate persist for so long a time during the first slow-growth period as during the second, whilst during the third period the growth-rate is so slow that it is practically negligible.



Text-fig. 4. Daily loss in length of frond in four populations of *L. saccharina*, showing the variation with age, season and habitat.

(1) Spring population, March 1942. Devon, exposed shore, intertidal zone (above M.L.W.S.T.).

(2) Spring population, April 1943. Devon, exposed shore, intertidal zone (above M.L.W.S.T.), in pools.

(3) Spring population, March 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

(4) Summer population, July 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

The numbers below each diagram give the month during which the frond tissue concerned was developed. R, rapid-growth period. S, slow-growth period.

Although the peak in growth-rate may vary with habitat and geographical position, the maximum rate of frond growth in length is reached in all populations during the second rapid-growth period in the life of a plant of this species;

the actual age in months at which the peak occurs being dependent on the time of germination of the plant.

For example, graphs 5 and 6 of Text-fig. 3 show the daily growth-rate of two groups of *L. saccharina* plants growing in the same habitat; in no. 5 development of the plants started in the spring (March), whilst in no. 6 development did not start until the summer (July). In the spring population the peak of growth is reached when the plants are about 15 months old, but in the summer population the peak is not reached until the plants are about 21 months old, 6 months later. Both peaks, however, occur during the second rapid-growth period in the two populations.

These figures show also that the rate of growth during the first rapid- and slow-growth periods varies in the two populations; the growth-rate is higher during the slow period in plants developed in the spring, but during the first rapid period the growth-rate is higher in plants that developed in the summer. Thus summer plants reach approximately the same length as 12- to 13-months-old spring-developed plants when they are from 9 to 10 months old.

The influence of *habitat* on the rate of frond growth in length of this species is very considerable, but to isolate with any certainty the influence of individual factors into which the habitat may be analysed is extremely difficult.

On all types of shore the general indications are that the rate of growth in length of the frond increases with decreasing level down to the upper sublittoral zone, where the maximum rate of growth is reached 1–4 m. below E.L.W.S.T. Although the growth in frond length has not been followed in individual plants growing below a depth of 4 m. below E.L.W.S.T., measurement of samples examined from depths down to 8 m. (Devon) and 12 m. (Argyll) showed that the rate of frond growth in length was less than at 4 m. below E.L.W.S.T. (Pl. VIII, fig. 33).

PLATE VIII. *Laminaria saccharina* (L.) Lamour.

Photographs of plants from different types of habitat. Figs. 25, 27 and 28 are of summer-developed plants growing on the Argyll coast in the intertidal zone in a fairly exposed habitat with emergence at low water of mean spring tides. Figs. 29–31 are of spring-developed plants growing on the Devon coast in the intertidal zone in a very exposed habitat with emergence at low water of mean spring tides. $\times \frac{1}{20}$.

Fig. 25. Six-months-old plant—sterile. 9. ii. 1943.

Fig. 26. Clump of plants up to 9 months old, from the same habitat as the series on Pl. V, showing different stages in frond regeneration and two plants bearing reproductive tissue. 30. xii. 1943.

Fig. 27. Ten-months-old plant—sterile. 20. vi. 1943.

Fig. 28. Eight-months-old plant—sterile. 22. iv. 1943.

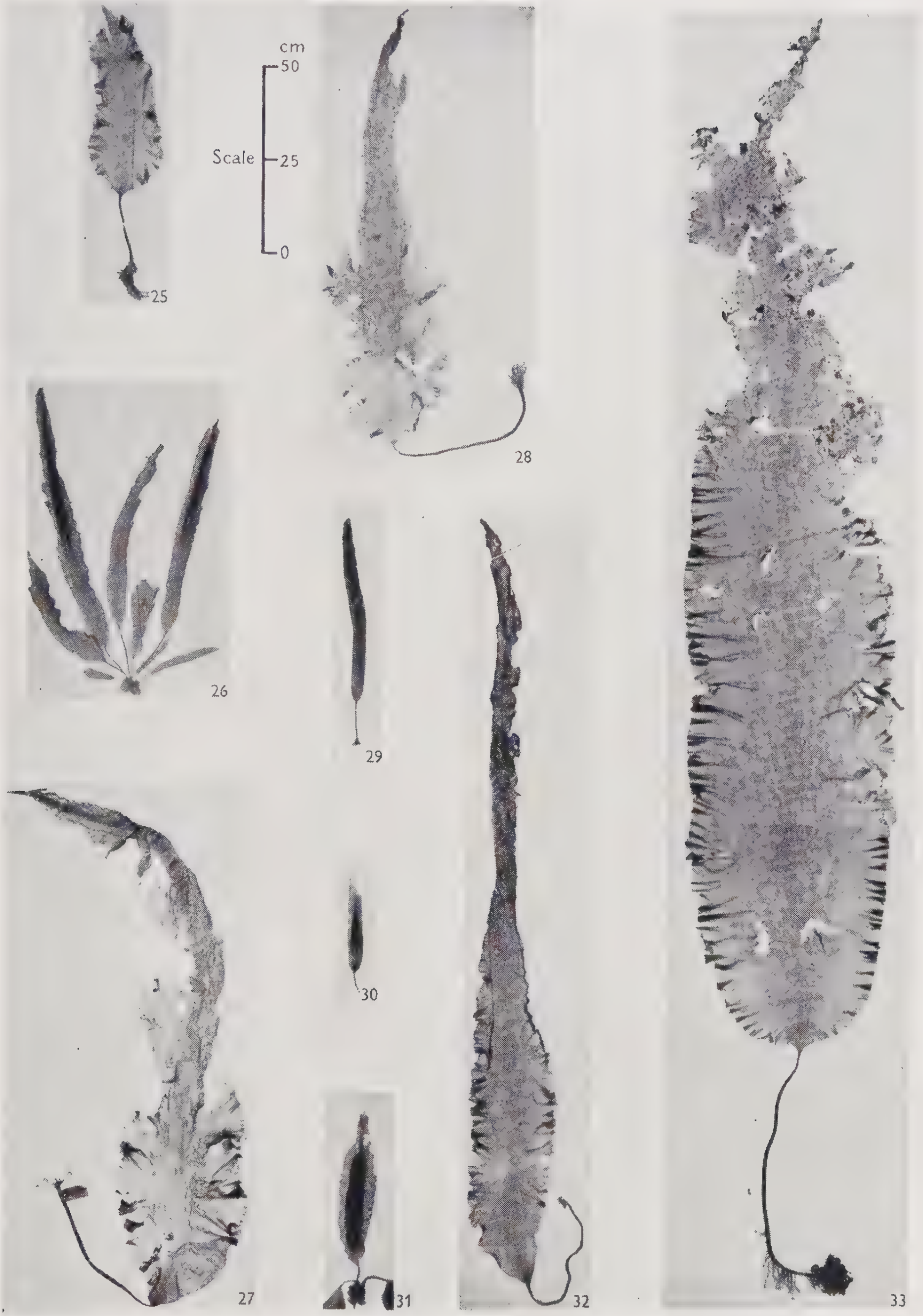
Fig. 29. First-year plant—immature reproductive tissue. 29. xi. 1943.

Fig. 30. First-year plant—mature reproductive tissue. 13. xii. 1943.

Fig. 31. Second-year plant—mature reproductive tissue. 28. xii. 1943.

Fig. 32. Plant approximately 1 year old—form of plant growing on raft in Plymouth Sound. 30. iv. 1943.

Fig. 33. Plant approximately 1 year old—form of plant growing on shingle off the Argyll coast at a depth of 12 m. below E.L.W.S.T. 5. vii. 1944.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Figs 25–33.

The records of the maximum growth figures show that at and above E.L.W.S.T. the daily growth in frond length never reaches a figure of 2 cm. increase a day during the rapid-growth period, whilst in the sublittoral zone a daily increase of up to 2·3 cm. can be obtained.

In addition to the effect of level on the growth in frond length the influence exerted by two other factors must be taken into consideration. The first of these factors is the degree of exposure or shelter of the habitat; the records show that the rate of growth in frond length increases with the degree of shelter of the habitat. The second factor is that of emergence or submergence of the plants during the period of low tide and concerns only habitats in the intertidal and sublittoral fringe zones. In these zones plants growing on the same shore and at the same level show a higher growth-rate if they remain continuously submerged (pool type), even under a very shallow covering of water, than do the plants which completely emerge during the period of low water (Pls. IX, X; Text-fig. 3, nos. 1, 4).

The variability in growth-rate in frond length during the third period of rapid growth, mentioned previously, is almost certainly connected with the depth of immersion of the plants and in consequence also with the factor of level on the shore. If the rates of growth during the second and third rapid-growth periods in the same populations are compared (e.g. in Text-fig. 3, nos. 1, 4 and 5), and if this is done for different habitats, the following points can be noted. On exposed coasts populations of plants growing in the intertidal zone above M.L.W.S.T. fail to survive the third period of rapid growth (Text-fig. 3, no. 1), showing only slight frond growth from the end of the second period of rapid growth until they disappear during the third period of rapid growth. The amount of frond length added in this type of habitat during the third rapid-growth period is approximately 4% only of the length of tissue added during the second period of rapid growth. Populations growing at the same level on the same shore but in pools, even in shallow pools of 30–50 cm. depth during the period of low water, survive the third period of rapid growth and show fair growth (Text-fig. 3, no. 4) during that period; the frond length added, however, during the third period is only 50–60% of that which is added during the second rapid-growth period. Finally, the populations growing in the upper part of the sublittoral zone (1–4 m. below E.L.W.S.T.) not only survive the third rapid-growth period but show a higher rate of growth during this period than do the two previous types mentioned, producing approximately 85% of the length developed during the second period (Text-fig. 3, no. 5). The difference in the frond growth-rate in these three populations during the third period of rapid growth is no doubt connected with the variation in the metabolism of the three populations, since Black (1948) has shown that the chemical composition of plants of the same *Laminaria* species varies at different depths of immersion.

To assess the *influence of geographical distribution* or of latitude on the growth of this species records of growth from many more stations would be required before any clear indication could be obtained. The figures available, however, for the growth of this species on the coasts of Devon (50° 18′ 20″ N., 4° 06′ 15″ W.) and Argyll (56° 14′ 22″ N., 5° 39′ 40″ W.) suggest, that over this portion of the species' range, the difference in the growth of plants in the two localities might be correlated with the difference in latitude; probably also with differences in the nature of the inshore water at the two stations.

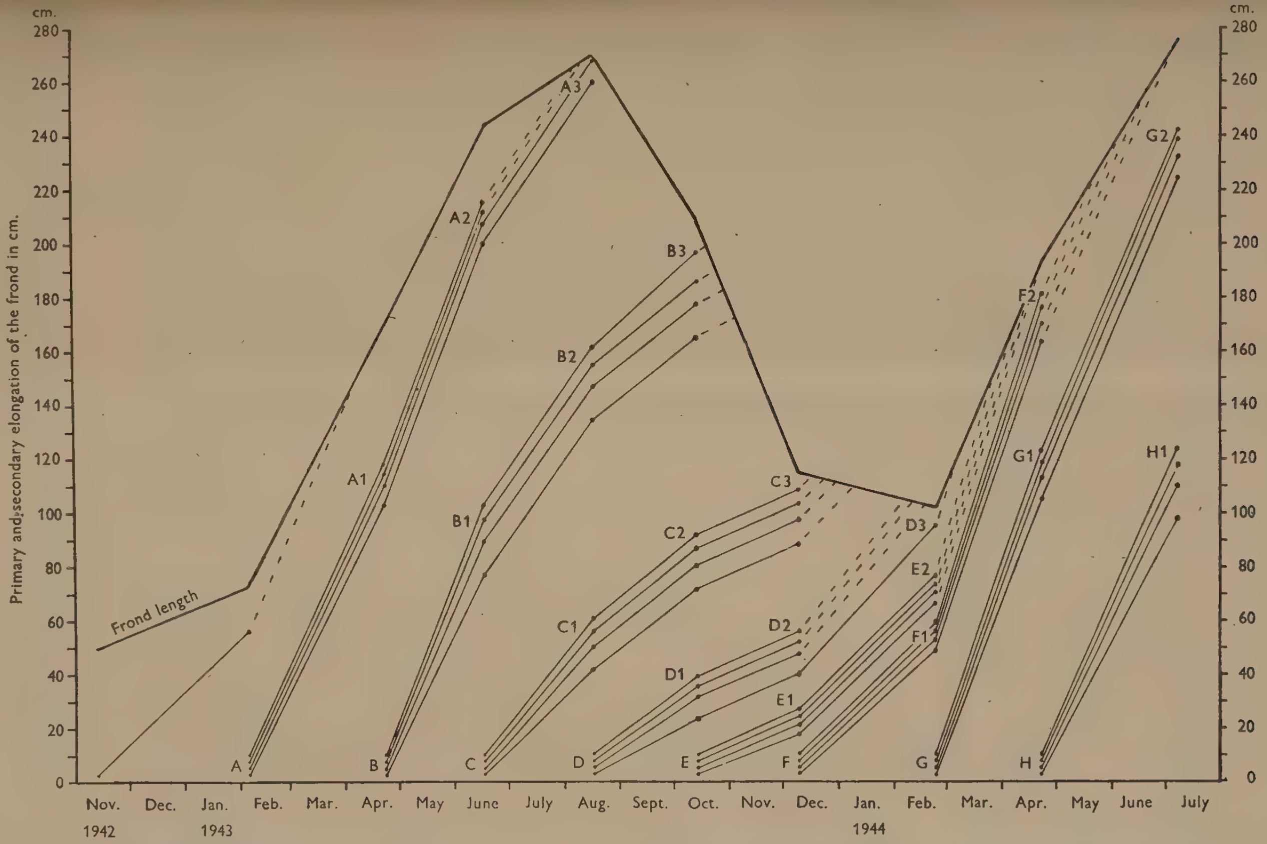
The differences noted are that, with an increase of approximately 6° in the latitude, there is a higher rate of frond growth throughout the yearly cycle at the more northern station; there also the time when the minimum and maximum rate of frond growth in length is reached is at least 1 month later than at the more southern station. An examination of the mucilage canals, in the same position on the frond in plants of the same age from the two stations (since Guignard (1892) has indicated these may vary in plants of different ages and in different parts of a single frond), shows that they are larger in the frond tissue of plants at the northern station than at the southern station. So also is the cell size of the frond tissue.

Primary and Secondary Growth in Length

So far the figures for frond elongation have been given as total increase in length for the whole frond and therefore do not show the differential growth-rate or elongation of the frond tissue at successive levels up the frond.

In this species, as in all Laminariales, the main growth region for increase in length is situated in the transition zone between the stipe and the frond, and so any tissue which forms below a level of 2·5 cm. above the base of the frond will be classed as *primary growth*, that is, new tissue formation, since below the 2·5 cm. level the differentiation of frond tissues is not complete, neither is the mucilage canal system developed. Above the 2·5 cm. level any increase in length of the tissues will be classed as *secondary growth*, this term including both increase in length by cell division and elongation by enlargement of the cells of the tissues already developed. Table IV and Text-fig. 5 give the primary and secondary elongation of frond tissue that took place in one plant from the age of 4 to 24 months, and illustrates the general method of frond growth in this species. The figures for elongation are obtained from the measurements of the distances between series of holes in the frond, punched at approximately 2-monthly intervals at 2·5, 5·0, 7·5 and 10·0 cm. up from the base (Pls. VI, VII).

Primary growth throughout the yearly cycles follows the general rhythm of periods of rapid and slow growth described earlier, the peak in primary growth being reached during the months of March and April, when a frond in the first and second rapid-growth periods can show a 54% and a 69% increase respectively per day in basal elongation. The minimum rate of growth for the



Text-fig. 5. Primary and secondary elongation of the frond in a plant of *L. saccharina* from the 4th to the 24th month of growth, illustrated by means of holes punched in the frond at 2·5, 5·0, 7·5 and 10·0 cm. above the base. Plant germinated July 1942 in the sublittoral zone on the Argyll coast at a depth of 1 m. below E.L.W.S.T.

primary growth region occurs during the months of November and December, when a 10·3% increase per day is shown in basal elongation.

Secondary growth in length takes place mainly in the zone 2·5–10 cm. above the base of the frond, also throughout the whole year. Above the 10 cm. level the proportion of frond tissue showing secondary growth, and the amount of that growth also, varies with the time of year.

The frond zone 2·5–10 cm. above the base follows a similar type of growth rhythm to that shown by the primary growth zone, but the growth in the former is at a much lower rate, with the rate diminishing upwards from the 2·5 to the 10 cm. level (Table IV). The rhythm of the growth-rate in this secondary growth zone lags behind that of the primary-growth rhythm, however, by about 2 months, so that the maximum rate is not reached in this zone until May and June, the rate remaining still high until August-September. The minimum rate, although reached in December, continues during January and February when the primary growth-rate has already started to rise.

In the frond tissue above the 10 cm. level secondary growth also follows the general rhythm of primary growth but without any time lag, and thus reaches the maximum rate at the same time as the primary growth zone during the months of March and April. At this time secondary growth in the tissue above the 10 cm. level can produce, during the second rapid-growth period in the life of a plant, 5% of the total increase in frond length. During the period of the minimum growth-rate of the primary growth tissue—November to December—there is no secondary growth in the frond tissue above the 10 cm. level. Thus the maximum increase (March-April) above the 10 cm. level occurs in tissue which is formed at the base during the minimum rate of primary and secondary (2·5–10 cm. level) growth (October to December), whilst the minimum rate above the 10 cm. level (October to December) occurs in tissue which is formed during the high growth-rates (June to August) of the primary growth tissue and the secondary growth tissue 2·5–10 cm. above the base.

From Table V, which gives the percentage increase in length of the tissue at the different levels of the frond from the base upwards, the method of growth in length of a frond can be followed. It can be seen that primary growth never drops below 72% of the total frond growth in length and that it shows the highest percentage of the total increase from October to April with the peak from December to February. The percentage of primary growth then

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PLATE IX

Growth in frond length, variation in frond width, and loss in frond length throughout the life of a spring population of *L. saccharina* growing intertidally on an exposed shore, on the South Devon coast, at 0·2 m. above M.L.W.S.T. (hence periodically uncovered). For explanation of figure see text, p. 667.

falls from April to October as the percentage of secondary growth in the 2·5–10 cm. zone above the base rises; the highest percentage increase in this tissue being recorded from August to October when the lowest percentage for primary growth is recorded. In the frond tissue above the 10 cm. level the highest percentage increase is from February to April in the tissue 3–4 months old with a decrease from April to June as in the primary tissue. In this tissue, however, the percentage increase then rises again from June to September before growth ceases during the months from October to December.

TABLE V. RELATIVE INCREASE IN FROND LENGTH AT DIFFERENT FROND LEVELS IN A PLANT OF *LAMINARIA SACCHARINA* FROM THE SEVENTH TO THE TWENTY-FOURTH MONTH OF GROWTH

	Percentage of total increase							
Growth periods ...	6. ii. 43– 22. iv. 43		22. iv. 43– 16. vi. 43		16. vi. 43– 16. viii. 43		16. viii. 43– 13. x. 43	
Secondary growth above the 10 cm. level in tissue:								
5–6 months old	—		—	0·4	0·4	1·6	0·0	1·4
3–4 months old	—		0·4		1·2		1·4	
Secondary growth:								
7·5–10·0 cm.	0·7	7·0	3·0	19·7	4·7	22·3	3·5	26·8
5·0–7·5 cm.	1·6		5·9		5·9		6·5	
2·5–5·0 cm.	4·7		10·8		11·7		16·8	
Primary growth:								
Base–2·5 cm.		93·0		79·9		76·1		71·8
Growth periods ...	13. x. 43– 10. xii. 43		10. xii. 43– 23. ii. 44		23. ii. 44– 22. iv. 44		22. iv. 44– 6. vii. 44	
Secondary growth above the 10 cm. level in tissue:								
5–6 months old	0·0	0·0	0·0	1·4	—	5·2	—	0·3
3–4 months old	0·0		1·4		5·2		0·3	
Secondary growth:								
7·5–10·0 cm.	1·7	10·8	0·6	4·7	1·2	8·7	3·3	16·5
5·0–7·5 cm.	3·0		1·1		2·5		4·9	
2·5–5·0 cm.	6·1		3·0		5·0		8·3	
Primary growth:								
Base–2·5 cm.		89·2		93·9		86·1		83·2

The frond growth illustrated above is of a plant growing on the Argyll coast; in plants growing on the Devon coast, however, the peaks of primary growth and secondary growth above the 10 cm. level are reached during February and March, and that of secondary growth at the 2·5–10 cm. level during April and May, the growth peaks, therefore, occurring a month earlier than on the Argyll coast.

Regeneration of the Frond

From the results of the experiments in which *L. saccharina* fronds were cut to a length of 5, 10 and 20 cm., and also by following the growth of labelled plants of known age from which the greater part of the frond had been torn off naturally, it has been found that complete regeneration of the frond does not occur in *L. saccharina* plants over 1 year old. Plants in the second and third year of growth may persist on the shore for a number of months after the fronds have been torn or cut if approximately 20 cm. of frond remains; they may also show a slight growth in length of the frond during that period, but they do not appear to survive through the winter months following the cutting or tearing of the frond.

During the first year of growth the younger the plant the more complete is the regeneration of the frond after cutting. Fronds of plants up to 3 months old can be cut to 10 cm. from the base at any time of the year and the fronds will regenerate in a few months to the size of the uncut fronds. This is probably due to the fact that in the young plants practically the whole of the growth in length is primary or basal growth. In plants between the age of 3 and 12 months, if tearing or cutting occurs during the rapid-growth period of this species (Pl. VIII, fig. 26) complete regeneration of the frond takes place in 6 months if from 15 to 20 cm. of frond is left on the plant. If less than 15 cm. of frond is left, or if the plants are cut during the period of slower growth, some regeneration does occur but the fronds always remain smaller than the uncut fronds of plants of the same age. When the whole frond is removed from a plant of any age no regeneration occurs, the stipe rots away gradually, and the holdfast eventually becomes detached from the substratum.

Experiments on the regenerative powers of *L. saccharina* carried out in 1920 on the French coast at Roscoff and at Iles Saint Quay by Freundler and Ménager (1921) gave results similar to those described above for second- and third-year plants. They state, however, that too young or too old plants were removed and not used in the experiments.

Fallis (1916), working from 15 June to 6 August 1915 on plants of the Laminariaceae, including *L. saccharina*, attached artificially to a floating raft in Friday Harbour, Washington, states that the cutting of the tip of the blade (frond) does not materially effect the growth so long as the basal 5–50 cm. of frond is left, and that larger plants grow faster than the smaller. The age of the 'larger' and 'smaller' plants, however, is not indicated.

Growth in Width

Variation in Width of Frond throughout Life of Plant

The width of the tissue developed by the fronds of plants of any age and in any habitat varies throughout a yearly cycle, as does the growth in frond

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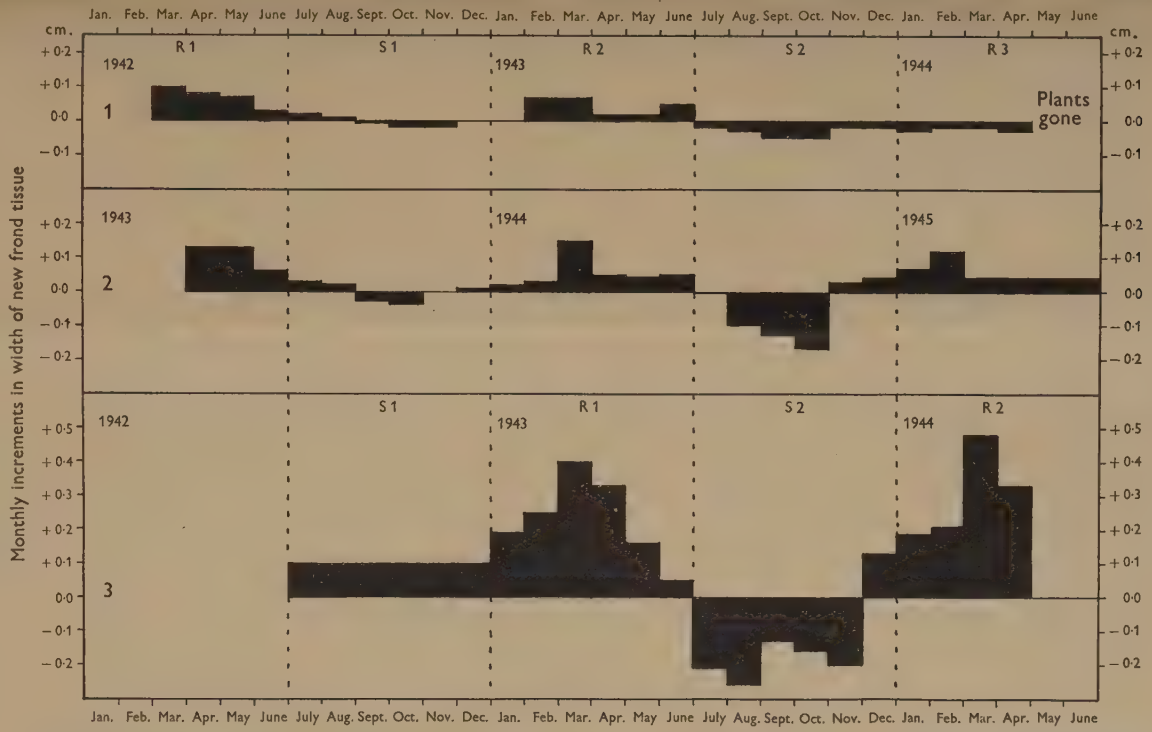
PLATE X

Growth in frond length, variation in frond width, and loss in frond length throughout the first 27 months of life of a spring population of *L. saccharina* growing intertidally on the same shore as in Pl. IX and at the same level, but remaining permanently submerged in pools. For explanation of figure see text, p. 667.



Text-fig. 6. Monthly increments in width of new frond tissue in three populations of *L. saccharina*, showing the variation with age, season and habitat. The figures, expressed in cm. per day, represent the difference (positive or negative) from the width of tissue produced during the previous month.

(1) Spring population, March 1942. Devon, exposed shore, intertidal zone, above M.L.W.S.T.
(2) Spring population, April 1943. Devon, exposed shore, intertidal zone (above M.L.W.S.T.), in pools.
(3) Summer population, July 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

R, rapid-growth period. S, slow-growth period.

length, increasing during the rapid-growth period of the species and decreasing during the slow-growth period (Pls. V–VII, IX–XI; Text-fig. 6). The thickness of the frond tissue produced also varies throughout a yearly cycle, the thickness decreasing during the rapid-growth period and increasing during the slow-growth period.

With the variation in the rate of growth in frond length and width throughout a yearly cycle a change takes place in the shape of the base of the frond so that the rapidity or slowness of the frond growth at any time can be assessed roughly from the shape of the frond base. When growth is extremely rapid the base is fusiform; as the rate of growth slows down the shape of the base alters from fusiform to cuneate; and then, when frond growth is at a very slow rate, the shape changes again from cuneate to nearly semicircular or subcordate (Pl. V). Yendo (1919), in his monograph on *Alaria*, also remarks on the change in shape of the base of the frond and considered it a remarkable process. He was of the opinion, however, that it was actually the same frond tissue changing shape, not realizing that new basal tissue was being produced whilst the old distal tissue was being cast off.

In addition to seasonal variation, the width and thickness of the frond also change with the age of the plant (Pls. IX–XI). Frond width during the second rapid-growth period of the plant is always greater and the frond tissue thicker than during the first period of rapid growth, but the width and thickness produced during the third period never exceeds that developed during the second. Maximum frond width, therefore, is reached at the same time as the maximum growth in frond length, that is, during the second rapid-growth period in the life of a plant (Pl. X), but the maximum thickness of the frond tissue is reached during the second period of slow growth.

The most rapid increase in the width of the frond tissue takes place during the period of the maximum primary growth in frond length between February and April; the frond tissue then increases in width at a slower rate until August in first-year plants and June in older plants (Text-fig. 6). Decrease in the width of the frond tissue produced, therefore, starts earlier, July, in plants over 1 year old, the rate of decrease being rapid until October or November (Pls. V–VII). In the first-year plants the decrease in frond width starts about 2 months later, lasts for a shorter time and is not so great as during the second slow-growth period (Pls. V–VII). The narrowing of the frond during the first slow-growth period is, therefore, hardly noticeable when the new frond tissue starts to increase in width at the beginning of the second period of rapid growth (Pl. V; Text-fig. 6).

PLATE XI

Growth in frond length, variation in frond width and loss in frond length throughout the first 24 months of life of a summer population of *L. saccharina* growing in the sublittoral zone on the Argyll coast in a sheltered habitat at a depth of 1 m. below E.L.W.S.T. For explanation of figure see text, p. 667.

In second-year plants, however, the constriction that appears in the frond due to the slow growth in length and great reduction in the width of the tissue produced during the second period of slow growth gives the impression, when the next rapid-growth period starts, of the so-called 'new frond' formation (Pls. V, VII, X and XI). If older plants are removed or become detached at any time of the year, the younger plants beneath, after a short period, give the same impression of 'new frond' formation as do the second-year plants, owing to the more rapid growth in length and width of the new frond tissue that has developed since the removal of the older plants.

Variation in Width of Frond with External Factors

In addition to the change in frond width with age of plant and season, variation also occurs in the width of the frond tissue with difference in bathymetric zone, habitat and geographical position. The statements made earlier in connexion with the variation in the rate of frond growth in length with changes in these factors hold good also for width variation, since with an increase in the rate of frond growth in length there is, in general, a corresponding increase in frond width, and with a decrease in length-rate, a decrease in frond width.

The width of the frond increases therefore, first, with fall in level down to the upper sublittoral zone where the maximum width is reached; secondly, with the increase in the degree of shelter of the habitat; and thirdly, from the southern to the northern station. The frond is also wider in intertidal plants that remain submerged, as compared with plants which are uncovered at low tides (Pls. V–XI; Text-fig. 6). Farlow (1882) also notes that in going northward on the east coast of North America the fronds of the plants of this species become broader.

For populations growing in the intertidal zone the figures show that during the second period of rapid growth there is, in addition to the maximum increase during February and March, a secondary rise in the rate of width increase during the month of June, the rate of increase having slowed down from March to May (Text-fig. 6). This secondary rise is more pronounced in populations with emergence at low tide, since the rate of width increase slows down more from April to May; it is accompanied in these populations by a corresponding rise in the rate of frond growth in length (Text-fig. 3). Populations that remain submerged during low water in the intertidal zone also show a slight rise in the rate of width increase during June (Text-fig. 6), but they show a decrease in the rate of frond growth in length from the previous month (Text-fig. 3). In the sublittoral zone no secondary rise in the rate of frond growth in length or width has been recorded.

Tikhovskaya (1940) has shown for *Laminaria saccharina* plants on the Russian coast that the coefficient assimilation/respiration reaches its maximum from February to May when photosynthesis is strongest; the coefficient decreases with diminishing energy of photosynthesis and increasing energy of respiration during the summer months, but in the autumn (October) a slight rise in the energy of photosynthesis is recorded. From his work he concludes that the temperature and light optimum of this species are low.

It can be seen from the foregoing facts that to give figures for the frond width of a *L. saccharina* population in any one habitat would be of little value, since during the time of maximum width production a variation in populations in different habitats and localities of from 9·5 to 45 cm. has been obtained on the Devon coast, and from 13 to 103 cm. on the Argyll coast.

Loss in Length

In this species loss of frond tissue from the distal end starts when a plant is a few months old and continues throughout the life of a plant (Pls. IX–XI; Text-fig. 4). The rate of frond loss from the apex in plants over 6 months old is such that the age of the oldest frond tissue varies normally between 5 and 7 months (Pls. X, XI), but in populations growing in exposed habitats in the intertidal and sublittoral fringe zones the average age of the apical frond tissue can drop to less than 4 months (Pl. IX). Frond tissue between 7 and 8 months old can survive on plants for short periods (Pls. IX, X), but in none of the populations examined has 9-months-old tissue been recorded (Text-figs. 8, 9).

Plants growing in the sublittoral zone show a more regular casting of apical frond tissue, according to the month the tissue was produced, than do plants growing in the intertidal zone (Text-figs. 3, 4). In the former zone frond tissue developed from January to June is cast from July-August to December, and that developed from July to December between January and July (Pl. XI). Since it is the frond tissue developed during the rapid-growth period of the frond that is cast from July-August to December in this zone, there is, therefore, a much heavier loss of frond tissue, both in length and weight during that period than during the period from January to June (Text-fig. 4, nos. 3, 4), and consequently the maximum frond length and weight for the year is reached between the months of June and July. There is a more definite tendency in plants in the intertidal and sublittoral fringe zones for the average age of the oldest frond tissue to vary with the season of the year, and to be slightly higher from October to March than from April to September; this retention of older frond tissue from October to March may be connected with the slowing down in the growth-rate and therefore the shorter frond length produced during the period (Pls. IX, X).

In intertidal populations also the rate of casting of frond tissue varies with the degree of exposure of the habitat. In extreme shelter the time of casting of the different months' frond tissue agrees with that found in the sublittoral zone. As the exposure of the habitat increases, the tissue produced during the months of slower growth is cast more rapidly (Pl. X; Text-fig. 4, no. 2), but the tissue developed from February to July is still cast between July and

February. With further increase in the exposure of the habitat the tissue produced in the early part of the rapid-growth period is also cast earlier until eventually, in exposed habitats, tissue developed from January to June (rapid growth) is cast from April-May to November-December, and that developed from July to December (slow growth) is cast between December and April (Pl. IX; Text-fig. 4, no. 1).

Frond loss in length from July to December is therefore still higher than from January to June in a habitat with medium exposure (Text-fig. 4, no. 2), but with greater exposure the amount of frond length lost from January to July is very little different from that lost between July and December (Text-fig. 4, no. 1). The maximum frond length and weight for the year in the intertidal and sublittoral fringe zones is reached at about the same time as in the sublittoral zone, or a little earlier, even when the frond loss is more evenly distributed throughout the year.

In all habitats plants in the first year of growth show some variation in the rate of frond loss due to the time of year at which they arise. On plants developed during the winter and spring sufficiently old frond tissue has been retained at the apex by the following September to November for the plants to follow the rhythm of frond loss of the older plants. In plants arising in the early part of the year the rate of growth during the slow-growth period is more rapid than in plants arising during the summer and autumn (Text-fig. 3, nos. 5, 6). Casting of apical frond tissue is more rapid, therefore, during the following spring and summer in plants developed during the summer and autumn than in plants developed during the previous winter and spring (Text-fig. 4, nos. 3, 4). This variation in the rate of casting of individual months' frond tissue in the first year of growth, due to the time of germination of a plant, has been shown to alter the age and the time of the year at which maturity is first reached in plants of this species. Plants over 12 months old, whatever their time of germination, follow the general rate of frond loss from the apex fairly consistently according to the habitat in which they are growing.

In this species also, whatever the time of germination, age or habitat of a plant, frond tissue produced from April-May to August-September is cast from the fronds during approximately the same period each year between October and March-April (Text-fig. 4). The variation, with time of germination of the plant and with habitat, in the time of casting of frond tissue developed between September and March-April appears to have an important bearing on the reproductive cycle of the sporophyte.

Growth of the Stipe and Holdfast

Before the sporeling of *L. saccharina* differentiates into stipe and frond it is attached by colourless rhizoids to the substratum. As differentiation proceeds an attachment disk develops at the base of the young stipe by cell multiplication. The first true haptera of the holdfast originate as outgrowths from this attachment disk, but later-formed haptera develop above the original haptera as outgrowths from the cortical tissue of the stipe.

The following zones can be recognized in a transverse section of a young stipe: a central medulla, surrounded by an inner and outer cortex, and on the outside of the cortex several layers of small cells, the outermost layer being an actively dividing meristoderm. A mucilage layer covers the meristoderm. Details of the structure of the stipe and of the development from the sporeling stage can be obtained from Drew (1910), Killian (1911) and Fritsch (1945).

Many workers, in particular Foslie (1884), Setchell (1900), Killian (1911), and Flerov & Karsakoff (1932), have drawn attention to the variation that occurs in stipe length and in the arrangement of the haptera of the holdfast in plants of the same species of *Laminaria* with variation in habitat and substratum, and have concluded that neither stipe length nor holdfast arrangement can be taken as criteria for specific distinction.

There are also many references in the literature (see Fritsch, 1945) to the periodic formation of new haptera series and to the ringed appearance of the stipe in the perennial Laminariales. The 'rings' in the stipes of the *Laminaria* species have not been studied except by Schultz-Schultzenstein (1853) and by Printz (1926) for *L. digitata* Lamour. Le Jolis (1855) does, however, correlate the 'ring' formation in the stipe of *L. cloustoni* with the annual increase in thickness which, he says, corresponds with a new whorl of haptera that is produced at the same time as a new frond. The growth of the stipe and the relation of the 'rings' in the stipe to both stipe and frond growth have not so far been followed in any species of *Laminaria*.

In the present work the growth in length of the stipe, the increase in stipe diameter and the development of the haptera forming the holdfast have been followed in all the plants of the different *L. saccharina* populations that have been studied for the growth of the frond.

The diagrammatic longitudinal sections of the stipe and holdfast on Pl. XII, illustrate the growth of both the stipe and holdfast up to the age of approximately 2 years in two populations of *L. saccharina*, an intertidal population growing on the Devon coast (frond growth in Pls. V and X) and a sublittoral population growing on the Argyll coast (frond growth in Pls. VI, VII and XI). In these figures the central medullary zone of the stipe is indicated by two lines; the dotted areas inside the medulla represent air pockets. The stippled areas indicate the tissue of the outer cortex of the stipe that is responsible for the darker 'rings' that show in a transverse section of the stipe. The outside lines represent the surface layers of small cells including, in the younger tissue, the outermost meristoderm layer.

General Rhythm in Rate of Growth

The growth of the stipe is similar to that of the frond in that it shows considerable variation in the rate of the growth during the different seasons of the year. The rhythm in the rise and fall in the rate of stipe and holdfast growth during a yearly cycle follows, fairly closely, the rhythm of the primary growth in frond length.

The figures on Pl. XII show that stipe growth in length and thickness is more rapid from January to June than from July to December with the maximum growth-rate between January and April and the minimum rate between September and November.

The figures show also that the formation of a new haptera series at the base of the stipe starts after the period of minimum growth, at the same time as the rise in the rate of stipe growth in length at the apex, the full haptera series completing its development by the end of the period of rapid growth. Normally, haptera series are not developed during the slow-growth period of the plant except, of course, in sporelings arising during that period, but after holdfast tissue has been eaten or damaged small secondary haptera may develop from the injured surface.

Variation in Rate of Growth

The same factors that appear responsible for the variation in frond growth seem to be responsible for the variation in the rate of stipe and holdfast growth that occurs among plants of this species, irrespective of the general rhythm in growth-rate that takes place during a yearly cycle. These factors are age and season of development of the plant, bathymetric zone, habitat and geographical position. An additional factor, the substratum, also influences the form and arrangement of the haptera of the holdfast.

Effect of Age

The influence of the age of the plant on the rate of stipe growth and the general sequence in stipe and holdfast development can be followed from the figures on Pl. XII.

After the young sporeling has differentiated into stipe and frond the primary growth in stipe length is from the apex and takes place by the cutting off of cells downwards by the formative or transition region between stipe and frond. A certain amount of secondary increase in stipe length by cell division and cell stretching occurs in the stipe tissue below the transition zone but at a diminishing rate downwards. The length of stipe tissue showing secondary increase depends on the rate of the stipe growth in length.

Increase in the diameter of the young stipe, holdfast region and haptera is due to the activity of the meristoderm or surface layer that cuts off cells inwards, thus increasing the thickness of the cortical tissue.

From July onwards, as the rate of growth of the stipe in length slows down during the period of slow growth, so also does the rate of increase in thickness, since the activity of the surface meristoderm also slows down, producing fewer cortical cells than during the period of rapid growth. The cortical cells produced during the period of slow growth do not reach the size of the cells formed during the rapid-growth period. The contents of these cells also appear denser, in some habitats darker brown. The denser and darker appearance may be due to the greater accumulation in the cells of physodes impregnated with fucosan, since the classical reaction of tannins was obtained with vanelin chlorohydrate. Except in the newly formed apical tissue in which the meristoderm retains its activity, there is a gradual decrease in the cell size of the cortical tissue produced until the activity of the meristoderm ceases in September or October, towards the end of the first period of minimum stipe growth.

Colour change in the surface of the stipe, holdfast region and haptera is an external indication of the change in the rate of stipe growth. When the growth-rate is rapid the surface tissue is light-coloured, but as the rate slows down the tissue darkens gradually, until at the end of the period of minimum growth, when the activity of the meristoderm ceases, the tissue is comparatively dark in colour.

After the minimum rate of stipe growth has been reached in the first slow-growth period there is, except in the newly formed apical stipe tissue, beneath the surface layers of the stipe, holdfast region and haptera a narrow layer of

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PLATE XII

Growth of the stipe and holdfast in two populations of *L. saccharina*. A, growth throughout first 27 months of life of a spring population in the intertidal zone (0·2 m. above M.L.W.S.T.) on the south Devon coast, in an exposed habitat, submerged at a shallow depth at low water of mean spring tides. B, growth throughout first 24 months of life of a summer population, growing in the sublittoral zone on the Argyll coast, in a sheltered habitat at a depth of 1 m. below E.L.W.S.T. For explanation see text, p. 684.

Notes

A, 1, first series haptera still forming, lower haptera attached.
2, first series haptera formed, majority attached.
3, first series haptera attached and darkening.
4, first series haptera dark.
5, beginning of second series of haptera.
6, first haptera of second series forming.
7, first haptera of second series formed, majority not attached.
8, first haptera of second series attached, further haptera forming above.
9, all haptera of second series formed, majority attached, pale in colour.
10, all haptera of second series attached and darkening.
11, 12, second series haptera dark.
13, beginning of third series of haptera.
14, haptera of third series forming.
15, third series haptera formed but not attached.
16, third series haptera attached.

B, 1, first series haptera formed, majority attached, pale colour.
2, beginning of second series of haptera, first series darkened.
3, first haptera of second series formed, some attached, further haptera forming above.
4, first haptera of second series attached, further haptera forming above.
5, all haptera of second series formed, majority attached, pale in colour.
6, all haptera of second series attached and darkening.
7, 8, second series haptera dark.
9, beginning of third series of haptera.
10, haptera of third series forming.
11, third series of haptera formed, majority attached, pale in colour

small-celled cortical tissue, the smallest cells being immediately inside the innermost cells of the surface layers. This cortical layer appears denser and more compact because of the smaller cell size of the tissue, and with further stipe growth in thickness will present the appearance of a darker 'ring' in a transverse section of a stipe (Pl. XIII, figs. 35, 36). This denser tissue will, in future, be referred to as 'compact' tissue or layer.

The stipes of plants that arise during the winter, spring and early summer show, after the first period of slow growth, a more definite compact layer than do the stipes of plants developed during the late summer and early autumn.

The first external indication of the start of the rise in rate of stipe and holdfast growth after the first minimum-growth period is the lightening in colour of both the apical part of the stipe below the transition zone and the base of the stipe immediately above the first haptera series. This colour change takes place from late October to early November.

At this time a layer of cells immediately outside the compact tissue starts to function as a secondary meristem. By the activity of this meristem new cortical cells, showing a radial arrangement, are produced on the outside of the compact layer. The secondary meristem first shows activity at the base of the stipe immediately above the first haptera series, and as its activity increases the original surface layers are cast off leaving the newly formed, lighter-coloured tissue at the surface. The change in colour at the base of the stipe indicates the activity of this secondary meristem and also the start of the formation of a new haptera series. At the apex the colour change is due to the more rapid rate in the growth in stipe length from the transition zone, and also to the increase in activity of the meristoderm that has remained functional in the apical part of the stipe.

By the end of December there is a further addition to the stipe length at the apex, but only a slight increase in the thickness of the new stipe tissue, whilst at the base of the stipe the first haptera of the second series can be observed as small protuberances. The activity of the secondary meristem has also spread upwards and downwards, so that a very narrow layer of new cortical tissue is present on the outside of the compact tissue part way up its length and below the new haptera down to the level of the first haptera series; the new growth frequently shows also on the outside of the proximal part of the uppermost haptera of the first series.

During January the activity of the secondary meristem continues to spread upwards on the outside of the compact tissue and the rate of stipe growth in length and thickness increases so that by February a layer of new cortical tissue is present on the outside of the whole length of the compact layer and there is an appreciable increase in the thickness of the young tissue of the stipe. At this time also the first haptera of the second series are fully grown, although the majority are not yet attached to the substratum and further haptera of the second series may be developing above those already formed.

From late February to April there is a very rapid increase in the rate of stipe growth (Pl. XII); the increase is shown in the new length of stipe added, in the increase in the thickness of all the young stipe tissue produced since the beginning of the rapid-growth period and also in the increase in thickness of the secondary cortical layer outside the layer of compact tissue (Pl. XIII, fig. 37). At this stage transverse sections of the stipe show, throughout the length of the compact layer, the new secondary cortical tissue as a lighter 'ring' or zone on the outside of the darker 'ring' of the compact layer (Pl. XIII, figs. 35, 36), whereas sections of the younger stipe tissue above the level of the compact layer show no 'ring' formation in the cortical tissue (Pl. XIII, fig. 34).

In the holdfast region the first-formed haptera of the second series are attached and further haptera are forming above them. The increased activity of the secondary meristem in the holdfast region below the level of the second haptera series is shown by the increase in width of the layer of secondary light-coloured cortical tissue on the outside of the compact layer of part of the holdfast region and on the outside of the proximal parts of the upper haptera of the first series. At this stage transverse sections of the uppermost haptera of the first series, taken near the point of origin from the stipe, show 'ring' formation (Pl. XIII, fig. 45).

PLATE XIII. *Laminaria saccharina* (L.) Lamour.

Photographs of sections of the stipe and holdfast. Figs. 34 and 35 are sections of the stipe of a plant from the same habitat as the plants illustrated on Pl. V. Figs. 36–45 are sections of the stipes of plants from the same blocks as the plants illustrated on Pls. VI and VII. Natural size.

Fig. 34. T.S. of stipe of 12-months-old plant taken from the stipe length produced during the second period of rapid growth. 28. iii. 1944.

Fig. 35. T.S. of stipe of 12-months-old plant taken from half-way up the length of the first compact layer. 28. iii. 1944.

Fig. 36. T.S. of stipe of 10-months-old plant taken from half-way up the length of the first compact layer. 22. iv. 1943.

Fig. 37. L.S. of base of the stipe and the holdfast of a 10-months-old plant. 22. iv. 1943.

Fig. 38. T.S. of stipe of 18-months-old plant taken from near the apex. 10. xii. 1943. See text, p. 691, for explanation of Figs. 38–41.

Fig. 39. T.S. of stipe of 18-months-old plant taken from the middle of the stipe length produced during the first rapid-growth period—medulla broken down. 10. xii. 1943.

Fig. 40. T.S. of stipe of 18-months-old plant taken from near the top of the length of the first compact layer. 10. xii. 1943.

Fig. 41. T.S. of stipe of 18-months-old plant taken from half-way up the length of the first compact layer. 10. xii. 1943.

Fig. 42. T.S. of stipe of 24-months-old plant taken near the top of the stipe length added during the first rapid-growth period. 6. vii. 1944.

Fig. 43. T.S. of stipe of 18-months-old plant at the end of the second slow-growth period. Section taken near top of first compact layer. 10. xii. 1943.

Fig. 44. T.S. of stipe of 18-months-old plant at the end of the second slow-growth period. Section taken half-way up length of first compact layer. 10. xii. 1943.

Fig. 45. L.S. of stipe and holdfast of 18-months-old plant at the end of the second slow-growth period showing the compact layer formed in the haptera during the first slow-growth period. 10. xii. 1943.

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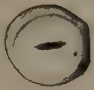
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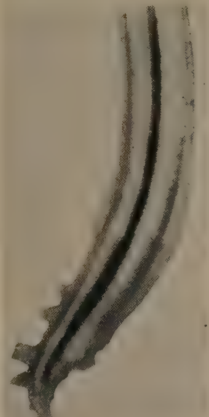
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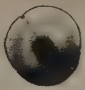
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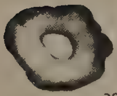
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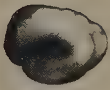
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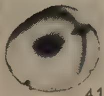
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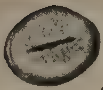
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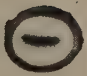
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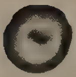
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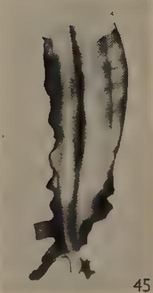
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Figs. 34–45.

distinguished from the older stipe length by the lighter colour of the surface tissues. The colour of this region is not so light, however, as the new stipe length that has developed during this rapid-growth period. Externally three colour zones can, therefore, be distinguished in the stipe at the end of the rapid-growth period following the second period of slow growth.

During the third slow-growth period the rate of growth in both stipe length and thickness is extremely slow, so slow in some plants that it is hardly discernible. The third compact layer that forms on the outside of the stipe and on the third series of haptera is therefore very narrow, and in many plants can be recognized only at the base and apex of the stipe.

The method of stipe growth in this species described above and figured on Pl. XII shows that, whatever the habitat, the approximate age of a *L. saccharina* plant can be assessed from an examination of the holdfast region (thick longitudinal section), since at this level the number of lighter and darker growth zones indicates the number of rapid- and slow-growth periods through which a plant has survived. The approximate length of stipe tissue formed during the first, second and third rapid- and slow-growth periods can also be obtained from a longitudinal section of the stipe. In the present work no evidence has been obtained from stipe and holdfast examinations to show that plants of this species persist on the British coast beyond the third period of slow growth.

The following points emerge from the observations on the growth of the stipe and holdfast in different-aged plants of this species. In plants arising early in the year the stipe length produced during the second period of rapid and slow growth is often equal to and seldom much less than that produced during the first period, but the length of stipe produced during the third period is always shorter than that produced during either of the two previous rapid- and slow-growth periods. The diameter of the stipe tissue produced during the second rapid- and slow-growth period is, however, greater than that produced during either the first or the third period of rapid and slow growth. Haptera development and secondary increase in thickness of the stipe also reach their maximum during the second period of rapid growth.

In plants arising later in the year, that is, during the slow-growth period of the species, the stipe length produced during the first slow- and rapid-growth period is always far greater than that produced during the second period. These plants go from the shore before the third period of rapid growth. The diameter of the stipe tissue produced during the first rapid-growth period is equal to if not greater than that produced during the second period. Haptera development and secondary increase in stipe thickness reach their maximum during the first period of rapid growth; thus the time of the maximum differs from that found in plants arising during the rapid-growth period of the species.

The stipes of the summer- and autumn-developed plants grow so rapidly in length and thickness during the first rapid-growth period that the development of the central medullary tissue does not keep pace with that of the cortical tissue and the medulla therefore becomes filled with air pockets (Pl. XII, B). In some plants the medulla breaks down completely in the rapidly growing part of the stipe and this part of the stipe becomes hollow; it also remains hollow throughout the life of the plant.

Pl. XIII, figs. 38–41, show transverse sections of the stipe of a summer-developed plant at the end of the second period of slow growth. From the base upwards the first section (fig. 41) is taken from halfway up the length of the first compact layer and the second section (fig. 40) from near the top of the first compact layer. The third section (fig. 39) is taken from the middle of the stipe length produced during the first rapid-growth period. This part of the stipe is hollow because of the complete breakdown of the medullary tissue. The fourth section (fig. 38) is taken from near the top of the stipe and is through the young stipe tissue in which the meristoderm has not ceased to function. The zone of less dense tissue on the outside indicates the beginning of the increase in activity of the meristoderm.

These summer-developed plants in which the apical part of the stipe becomes hollow agree with the description given by Børgesen (1903) for the species *Laminaria faeroensis*.

The sequence of the variation in the rate of growth of the stipe in plants arising during the rapid-growth period agrees fairly closely with the sequence that occurs in the rate of growth of the frond with change in age of the plant. Although the length of stipe tissue produced during the first rapid-growth period may be greater than the length produced during the second rapid-growth period, the actual amount of stipe tissue added, that is, in length, thickness, secondary thickness and haptera, is greater during the second rapid-growth period than during the first. As in the frond growth, the rate of stipe and holdfast growth during the third rapid-growth period varies considerably in populations growing in different habitats, but it is always less than the rate of growth of the stipe and holdfast during the second rapid-growth period. During the slow-growth periods the sequence in the rate of stipe growth is also in accord with that found in the frond except that the minimum rate is reached slightly earlier than in the frond.

For plants arising during the slow-growth period it has been shown that the growth-rate of the frond is higher during the first rapid-growth period than in plants arising during the early part of the year. The rate of stipe growth is also higher during the first rapid-growth period in plants arising during the slow-growth period, but unlike the rate of growth of the frond which increases during the second rapid-growth period, the rate of stipe growth is not so great during the second as during the first period of rapid growth.

Effect of Habitat

Habitat influences the rate of growth of the stipe and holdfast as it does the rate of growth of the frond (Pls. V–VIII). As in the frond the general indications are that the rate of stipe growth increases with the degree of shelter of the habitat, with submergence of the plants as against emergence at low water, and with fall in shore-level down to the upper sublittoral zone. The maximum rate of stipe growth is reached 1–4 m. below extreme low water of spring tides.

At and above the level of E.L.W.S.T. the growth in length of the stipe never reaches a 0·3 cm. increase a day during the rapid-growth period, whereas in the sublittoral zone the daily increase in stipe length can reach a figure of 0·5 cm. The measurements of stipes of plants of this species growing on the Devon and Argyll coast show that the range of stipe size is very great. On exposed shores in the intertidal zone in habitats that dry out at low water the stipe of a plant at the end of the second slow-growth period may be less than 10 cm. long with a diameter of 0·5 cm., while plants of the same age growing in the sublittoral zone on sheltered coasts may have a stipe length of up to 130 cm. with a diameter of 1·9 cm.

The tissue of the slow-growing stipes, particularly that formed during the slow-growth periods, is much darker in colour than the tissue of the more rapidly growing stipes. This colour variation of the stipe tissue in plants growing in different habitats may be due, partly to the smaller cell size of the tissue in slow-growing stipes, and partly to variation in chemical composition of the stipe tissue of plants growing at different levels on the shore. Black (1948) working on *Laminaria* spp., Russell-Wells (1932) and Haas & Hill (1933) working on *Laminaria* and other genera have shown that there is a variation in the chemical composition with the degree of emergence and the depth of immersion of the plants.

The variability in frond development during the third period of rapid growth in populations of this species growing in different habitats has been connected with depth of submergence of the plants. Stipe and holdfast development during the third period of rapid growth also shows variability with difference in depth of submergence of the plants. In populations growing in the intertidal zone in habitats that dry out at low water of mean spring tides growth of the stipe and holdfast practically ceases early in the second period of slow growth. The third haptera series, therefore, is not produced, and on exposed coasts the plants fail to survive the third period of rapid growth.

In populations growing at the same level in the intertidal zone but in pools there is usually a slight increase in stipe length during the third period of rapid growth and a third haptera series is also formed, but the haptera are small and very few in number. In populations growing in the upper part of the sublittoral zone, however, there is, during the third period of rapid growth, an appreciable increase in stipe length and a fuller development of the third haptera series.

In this species the form of the holdfast depends on the nature of the substratum on which the plant is growing. The variation in form that can occur with variation in the character of the ground has been dealt with in detail by Flerov & Karsakoff (1932). In general, the two extremes of form occur on rock and on soft silty ground. On rock the holdfast is compact with the haptera thick and only slightly branched (Pls. V; VIII, figs. 26, 29), while on soft silty ground the holdfast is much less compact and the haptera are thinner, longer and very copiously branched (Pl. VIII, fig. 33). All gradations between the two extreme forms can be obtained on different types of ground.

Geographical Variation

The figures for the growth of the stipe and holdfast of this species on the coasts of Devon and Argyll suggest that the difference in the growth of the stipe and holdfast in the two localities might also be correlated with difference in latitude. There is a higher rate of growth at the more northern station, and only at this station is the stipe growth so rapid that the medulla breaks down completely, leaving the stipe hollow. At this station also the maximum rate of stipe growth is reached in April and the minimum rate in October, while at the more southern station the maximum rate is reached in March and the minimum rate in September, approximately one month earlier than at the more northern station.

The results of the work on the growth of the sporophyte of *L. saccharina* on the Devon and Argyll coasts have shown that there is, within the plant itself, some dominant factor controlling the rhythm of its development, but that there are also factors external to the plant that may modify, very considerably, the morphological and anatomical character of the species.

Information from localities round the greater part of the British coast is still needed before a full knowledge of the variation in form of this species with change in its geographical position on the British coast can be assessed.

Records of the growth and behaviour of the species throughout its total range are also necessary before the full influence of latitude, direct or indirect, on the behaviour of the species can be understood, since, according to Wimpenny (1941), one algal group, the Dinophyceae, shows an increase in size with increase in latitude, whilst in another group, the Bacillariophyceae, the marine pelagic forms decrease in size with increase in latitude.

REPRODUCTION IN THE SPOROPHYTE

In the literature very little information is available on the reproductive period of the sporophyte of *L. saccharina* on different parts of the British coast. It is recorded by Rees (1928) for the Aberystwyth and Gower coast as occurring from October to early April; these records are for plants growing in the intertidal zones in habitats that dry out during low water of spring tides. During the period 1923–27 he found no plants fruiting from late April to September; the main fruiting was from November to the end of February, the peak being reached during either January or February. Harries (1932) states that during 1929–30 reproduction in *L. saccharina* at Aberystwyth started early in November and ended early in March (Text-fig. 7, no. 2*b*), but in a less exposed region, St Davids, reproduction started a month earlier than at Aberystwyth. Knight & Parke (1931) record the production of reproductive tissue during all seasons of the year on plants growing on the coast of the Isle of Man.

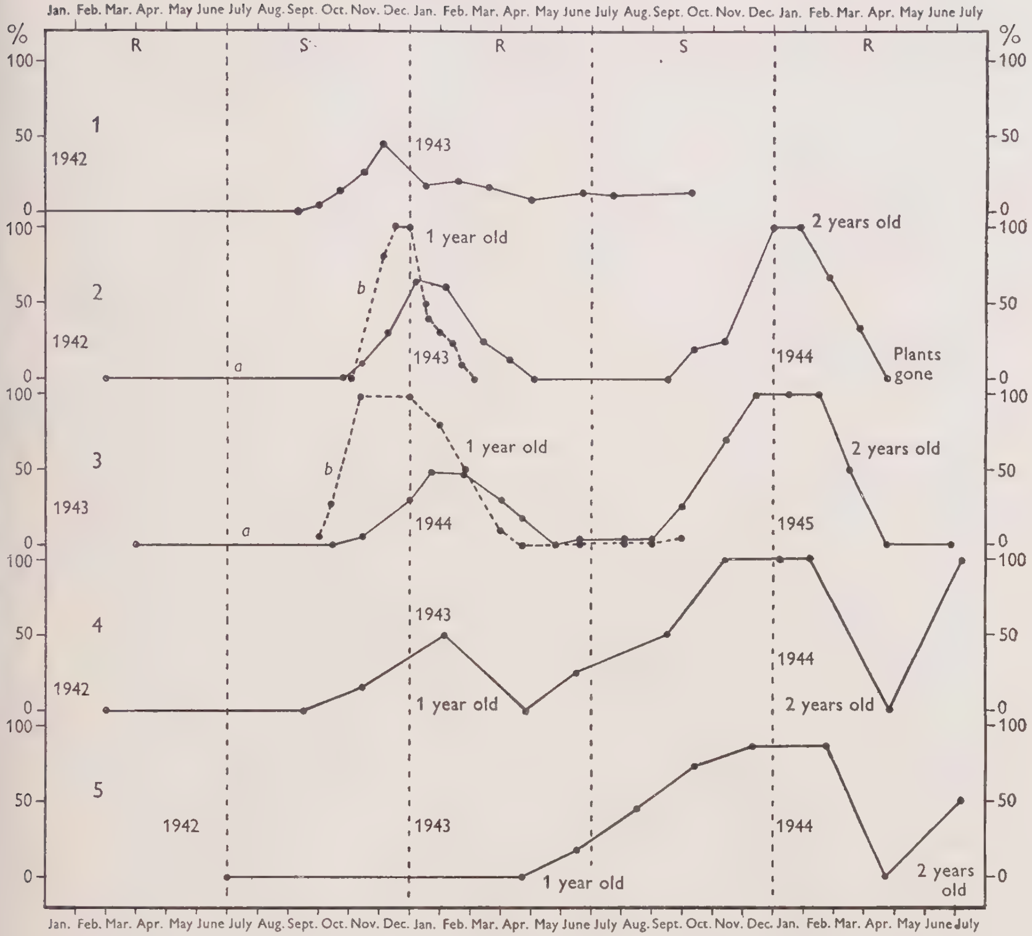
On the French coast Sauvageau (1918) found reproductive tissue on adult plants at all times of the year, whilst Børgesen (1903), during the period from May to November, found fructifying specimens in the Faeröes only during the months of June and July. On the Norwegian coast, in the Trondheim Fjord, Printz (1926) found reproducing plants in the middle of May and at the end of September and concludes that the sporogenous tissue becomes detached gradually from the frond during the autumn, whereas further north, on the East-Finmarken coast, according to Foslie (1890), reproduction occurs in the winter or early in the spring. For the Arctic, Kjellman (1883) states that on the coast of the Polar Sea sublittoral varieties only bear zoosporangia during July, August and early September, the varieties at and near low-water mark being sterile during this period. According to Kireeva & Schapova (1933, 1938) reproduction of this species on the Murman coast starts in July, reaches a maximum early in August and finishes at the end of August.

The present work has shown that on the coast of Devon and Argyll plants of this species can be found bearing reproductive tissue during all months of the year; in all populations, however, the percentage of reproducing plants is highest between the months of October and March (Text-fig. 7).

Contrary to the findings of Kireeva & Schapova (1933, 1938), who state that *L. saccharina* does not reach maturity on the Murman coast until the third year of growth, this work has shown that on the British coast reproductive tissue first develops on the fronds when the plants are from 8 to 12 months old (Pl. V, figs. 2, 3; Pl. VIII, fig. 26). Plants that develop during the early part of the year can start to bear reproductive tissue when they are 8–9 months old, but plants developed later in the year do not form reproductive tissue until they are nearly 1 year old. The plants, therefore, that start life during the rapid-growth period of the species reach maturity approximately 4 months earlier than do plants that start life during the period of slow growth.

Development of Reproductive Tissue

For reproductive tissue to develop on a frond of a *L. saccharina* plant the distal tissue present on the frond must be in at least the sixth month of growth. Once reproductive tissue is present on frond tissue in the sixth month of growth, it can arise also on frond tissue in the fifth month of growth. If how-



Text-fig. 7. Periodicity of reproduction in different populations of *L. saccharina*, showing the variation with age, time of germination, habitat and locality. The graphs start at the month when the plants germinated (except graphs 1, 2*b* and 3*b*).

(1) Population on floating raft. Plymouth Sound, Devon, sheltered habitat, shallow submergence permanent. First sporophytes germinated December 1941–January 1942 and new sporophytes added each succeeding month; all sporophytes, including sporelings, counted in samples examined for percentage reproduction in population.

(2*a*) Spring population, 1942. Devon, exposed shore, intertidal zone, above M.L.W.S.T. (thus periodically uncovered).

(2*b*) Normal population. Aberystwyth, 1929–30. Figures given by Harries (1932).

(3*a*) Spring population, 1943. Devon, exposed shore, intertidal zone (above M.L.W.S.T.), in pools (thus never uncovered).

(3*b*) Normal population, 1943–44 (chiefly plants in second and third year of growth—very few first-year plants). Devon, exposed shore, intertidal zone (above M.L.W.S.T.), in pools.

(4) Spring population, 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

(5) Summer population, 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

R, rapid-growth period. S, slow-growth period.

TABLE VI. THE PRODUCTION OF REPRODUCTIVE TISSUE IN RELATION TO THE AGE OF FROND TISSUE IN A SPRING POPULATION OF *LAMINARIA SACCHARINA* DEVELOPED ON THE DEVON COAST IN MARCH 1942 IN THE INTERTIDAL ZONE, ABOVE M.L.W.S.T. (THUS PERIODICALLY UNCOVERED)

Age of frond tissue in months	Number of plants Without brackets—with sterile tissue With brackets—with reproductive tissue												
	1943 Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	1944 Jan.	Feb.	Mar.	Apr.
1	8	5	5	5	5	5	5	4	4	3	3	3	1
2	8	5	5	5	5	5	5	4	4	3	3	3	1
3	7	5	5	5	5	5	5	4	4	3	3	3	1
4	7	2	5	5	5	4	5	4	4	3	3	3	1
5	1	—	1	4	5	4	3 (1*)	3 (1*)	(4*)	(3*)	(2)	3	1
6	(1)	—	—	—	—	4	3 (1)	2 (1)	(4)	(3)	(2)	(1)	1
7	—	—	—	—	—	—	—	—	(1)	(2)	(2)	(1)	—
8	—	—	—	—	—	—	—	—	—	—	(2†)	—	—
9	—	—	—	—	—	—	—	—	—	—	—	—	—

* Immature reproductive tissue. † Liberation of zoospores nearly finished.

TABLE VII. THE PRODUCTION OF REPRODUCTIVE TISSUE IN RELATION TO THE AGE OF FROND TISSUE IN A SUMMER POPULATION OF *LAMINARIA SACCHARINA* DEVELOPED ON THE ARGYLL COAST IN JULY 1942 IN THE SUBLITTORAL ZONE AT A DEPTH OF 1 m. BELOW E.L.W.S.T.

Age of frond tissue in months	Number of plants Without brackets—with sterile tissue With brackets— with reproductive tissue									
	1942 Nov.	1943 Feb.	Apr.	June	Aug.	Oct.	Dec.	1944 Feb.	Apr.	June
1	25	20	20	20	11	11	10	7	5	4
2	25	20	20	20	11	11	10	7	5	4
3	25	20	20	20	11	11	10	7	5	4
4	25	20	20	20	11	11	10	7	5	4
5	25	20	14	20	5 (5*)	3 (7*)	(9*)	(6*)	5	4
6	—	8	12	12 (4*)	3 (5)	3 (5)	(9)	(6)	5	1 (3*)
7	—	—	—	(4)	(2)	(7)	(8)	(5)	(3†)	(3)
8	—	—	—	—	—	(2†)	(2†)	—	—	—
9	—	—	—	—	—	—	—	—	—	—

* Immature reproductive tissue. † Liberation of zoospores nearly finished.

ever it arises on frond tissue in the fifth month of growth it does not usually mature until the beginning of the next month (Tables VI–VIII; Text-figs. 8, 9). The evidence available indicates that reproductive tissue is produced only on frond tissue that is approaching or has reached final expansion. Since considerable expansion occurs during the spring months in frond tissue in the fifth and sixth month of growth, during the period of maximum increase in frond length above the 10 cm. level, production of reproductive tissue during this period is at a minimum.

It takes from 14 to 21 days for reproductive tissue to develop and reach maturity in this species. There is no perceptible variation in the time taken for reproductive tissue to develop with differences in the age and habitat of the plant, or with the season of the year. Once reproductive tissue has reached maturity it can continue to liberate zoospores for 2–3 months if the frond tissue bearing it is retained by the plant.

Table VIII. The Production of Reproductive Tissue in Relation to the Age of Frond Tissue in a Spring Population of *Laminaria saccharina* developed on the Devon Coast in April 1943 in the Intertidal Zone (above M.L.W.S.T.) in Pools

Age of frond tissue in months	Number of plants Without brackets—with sterile tissue With brackets—with reproductive tissue						
	1944				1945		
	June	July	Aug.	Sept.	Jan.	Feb.	June
1	34	32	29	24	5	4	3
2	33	30	26	24	5	4	3
3	32	26	23	19	5	4	3
4	27	24	22	19	5	4	3
5	23	24	21	13 (6*)	(5*)	(4*)	3
6	3 (1)	3 (3)	1 (1)	8 (6)	(5)	(4)	—
7	—	—	—	(2)	(3)	(3)	—
8	—	—	—	—	(2†)	(1†)	—
9	—	—	—	—	—	—	—

* Immature reproductive tissue. † Liberation of zoospores nearly finished.

When reproductive tissue first reaches maturity it bears approximately 1,000,000 ripe sporangia per cm.^{2} of frond surface. Sporangium initial cells and immature sporangia are not included in the above figure. A fortnight to a month after the first liberation of zoospores, the number of ripe sporangia is about 500,000 per cm.^{2} of frond surface. During the second and third months after the first liberation of zoospores there is a further drop in the number of ripe sporangia present on the reproductive tissue, although new sporangium initial cells continue to develop and mature, frequently inside the walls of sporangia from which the zoospores have been liberated. Kireeva & Schapova (1938) give 562,500 as the number of sporangia per cm.^{2} of frond surface on plants of this species growing on the Murman coast.

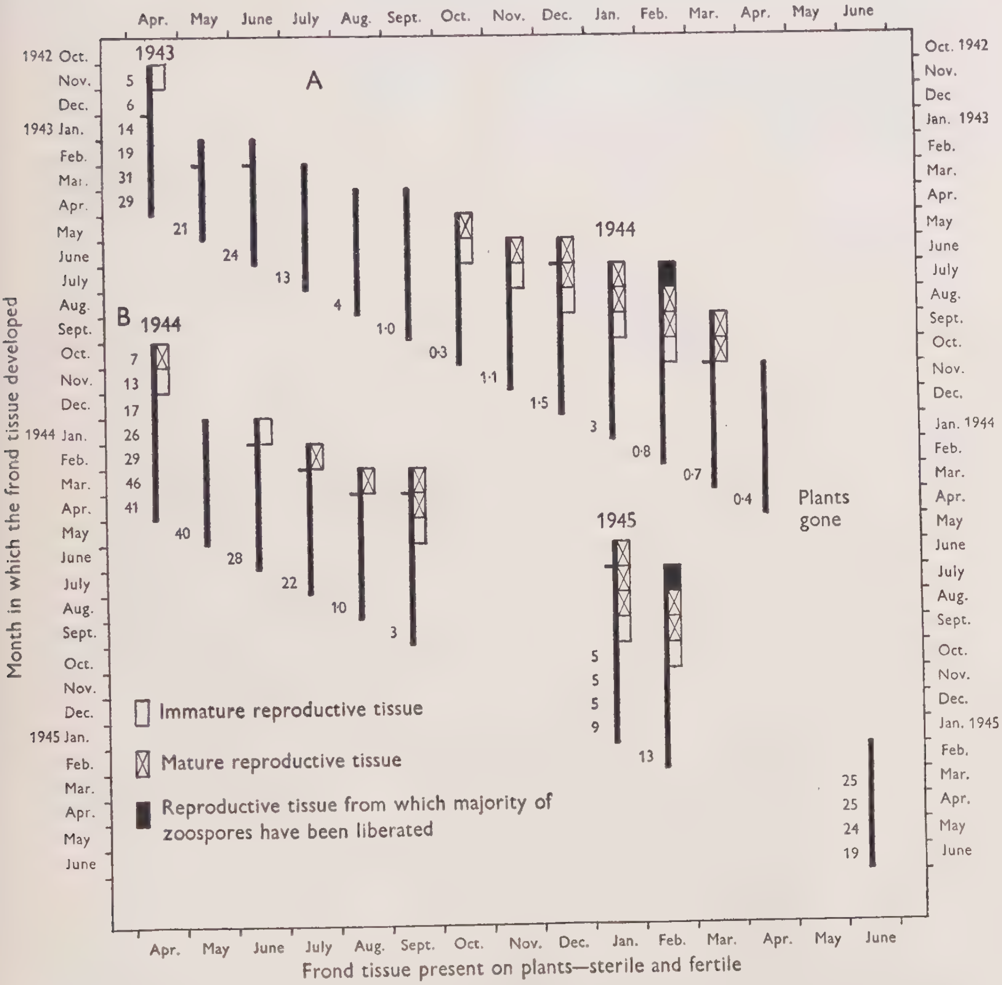
The number of zoospores produced by one sporangium is 32; this figure agrees with that given by Schreiber (1931) for plants growing at Heligoland, but not with that given by Kireeva & Schapova (1938) who state that the sporangia developed on plants on the Murman coast produce 64 zoospores.

Drew (1910), working at the Plymouth Laboratory, obtained 2,000,000 gametophytes from 1 sq. in. of reproductive area of the frond, whilst from Kireeva's and Schapova's (1938) figures it can be estimated that 36,000,000 zoospores are produced per cm.^{2} of frond surface of plants on the Murman coast. The above figures, however, are the numbers of zoospores, or the gametophytes developed from the zoospores, produced by the reproductive tissue on the frond at one time.

If reproductive tissue is retained for a sufficiently long period on the frond, it develops successive crops of sporangia. It has been estimated that if reproductive tissue can persist on the frond for 3 months after it first reaches maturity, 1 cm.^{2} of frond surface bearing reproductive tissue can produce up to 2,000,000 sporangia. This means that if reproductive tissue is retained on a plant until the frond tissue bearing it is in the eighth month of growth, 1 cm.^{2} of frond surface can liberate 64,000,000 zoospores over a period of 3 months. It is, however, only for a short period during the year that frond tissue in the eighth month of growth is retained by plants of this species (Tables VI–VIII). In the intertidal and sublittoral fringe zones frond tissue in the seventh month of growth also does not persist on the plants for more than 6 months of the year, frequently for a much shorter period (Tables VI, VIII; Text-fig. 8).

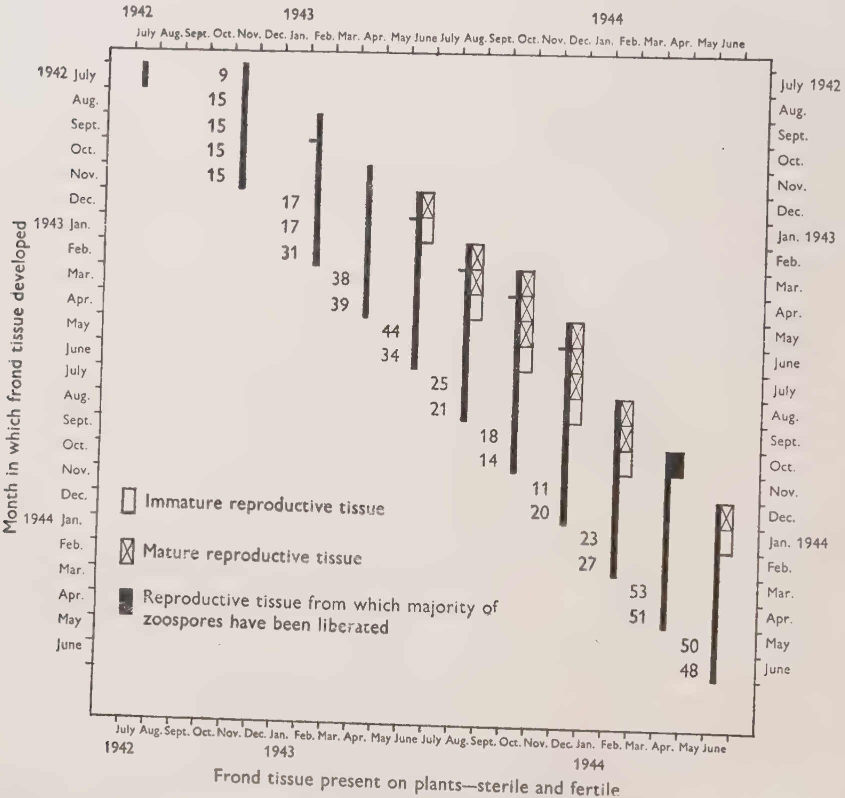
There is, therefore, a certain wastage of potential reproductive products in plants of this species, particularly in plants growing in the intertidal and sublittoral fringe zones. The wastage, however, is not more than about 25% of the total number of zoospores that could have been produced if the frond tissue had survived beyond the age of 6 months, since the number of sporangia developed diminish rapidly with each successive crop that is produced. On any frond tissue 50% of the total number of zoospores that can be produced during 3 months are released when the tissue first reaches maturity in the sixth month of growth and another 25% by the end of the sixth month or early in the seventh month, leaving only 25% of the total number that can be produced by the tissue for release during the seventh and eighth months of frond growth.

As frond tissue formed during any month of the year has to reach a certain age and certain stage in development before it can bear reproductive tissue, the frond tissue produced during any one month of the year by all plants of this species will bear reproductive tissue at approximately the same time of the year if it persists on the plants (Text-figs. 8, 9). At any time of the year, therefore, the proportion of the frond length bearing reproductive tissue in plants of this species is obviously dependent on the rate of growth in length of the particular frond, the rate of casting of its distal frond tissue, and the particular month's or months' frond tissue that is bearing the reproductive tissue (see Text-figs. 8, 9 with figures for frond length in cm. at side of



Text-fig. 8. The relation of age and time of development of frond tissue to the production of reproductive tissue on the fronds of two intertidal spring populations of *L. saccharina*. The black column represents frond tissue present on plants; the maximum amount is given by the full length of the line, the average amount marked on the *left* by a short protruding line. Those parts of the frond which have reproductive tissue are clearly marked by the rectangles projecting on the *right* side of the column. Figures at the side of the columns indicate the length of frond tissue (in cm.) developed during that month. Devon, exposed shore, intertidal zone; A, above M.L.W.S.T. (from 14th to 25th month of life); B, at same level in pools (from 13th to 27th month of life).

columns). Throughout a yearly cycle, the frond tissue formed during the period of rapid growth will produce a greater proportion of reproductive tissue, and therefore a greater number of zoospores, than the frond tissue formed during the period of slow growth, providing these tissues persist on the plant until they reach maturity (Text-figs. 8, 9). There is not only a greater length but also a greater width of reproductive tissue produced on frond tissue that has developed during the period of rapid growth, since the width of sporangial tissue formed on a frond appears to be proportional to the width of the frond tissue itself, increasing with increase in the width of the frond.



Text-fig. 9. The relation of age and time of development of frond tissue to the production of reproductive tissue on the fronds in a sublittoral summer population of *L. saccharina*, growing on the Argyll coast in a sheltered habitat at a depth of 1 m. below E.L.W.S.T. Explanation as in Text-fig. 8.

In any habitat, therefore, the maximum production of reproductive tissue takes place in a second-year plant since the peak of frond growth in length and width is reached during the second year of growth. There is also variation in the amount of reproductive tissue produced by plants growing in different habitats and at different latitudes, the area of reproductive tissue produced by the plants increasing with decrease in level on the shore, with increase in the shelter of the habitat, and with increase in the latitude. Considerable variation is, therefore, to be found in the shape, area and position of the reproductive tissue that develops on the fronds of plants of this species (Pls. V–VIII).

PERIODICITY OF REPRODUCTION

As the age of the distal frond tissue on a first-year plant is controlled more by the time of development of the plant and the resulting initial rate of growth during the first 6 months than by factors external to the plant, the time of the year that reproductive tissue first develops on a plant is controlled also by the time of the year the plant starts to develop.

In a plant over 12 months old, however, the age of the distal frond tissue depends on the degree of exposure or protection afforded to the plant by the habitat in which it develops. The period during which a plant can produce reproductive tissue depends, therefore, on the nature of the habitat in which the plant is growing; the reproductive period is extended in sheltered habitats and curtailed in exposed habitats.

Throughout a yearly cycle, therefore, the duration of the reproductive period in any population of *L. saccharina*, and the percentage of that population bearing reproductive tissue during the reproductive period, depend on two factors, the type of habitat in which the population is growing and the numbers of the different season and year groups making up the population.

As frond tissue developed from April-May to August-September is cast in all plants of this species between the months from October to March-April, and as the age of the oldest frond tissue in all plants is higher from October to March than from April to September, the maximum production of reproductive tissue will take place in all populations, whatever the type of habitat, from October to March on the frond tissue developed from approximately April to September (Text-fig. 7). It is, therefore, the extension of the reproductive period of a population beyond October to March that is controlled by the two factors, the habitat and the components of a population.

Earlier in this paper, production, longevity and depopulation-rate of the sporophytes were related to bathymetric zone and degree of exposure of the habitat, therefore the components of any population, at any season, depend also on the habitat factor. The nature of the habitat of a population is therefore the controlling factor for the production, or lack of production, of reproductive tissue on the plants during the period from April to September.

The nature and locality of the shore examined by different workers is no doubt responsible for the apparent discrepancy given in the literature in the records of the time of reproduction of this species.

On the British coast, throughout a yearly cycle, the reproductive period of this species is shortest (October to early April) in populations growing on exposed shores in intertidal habitats that dry out at low water of mean spring tides (Text-fig. 7, nos. 2*a*, *b*).

In these habitats, the persistence of just the spring sporophytes (Table III) that first reach maturity during the autumn and winter following their germination (Text-fig. 7, no. 2*a*) and the rapid casting of the frond tissue from April to September in the second-year spring plants (Pl. IX; Text-fig. 8A), so that frond tissue sufficiently old to bear reproductive tissue is not retained by the plants (Table VI; Text-fig. 8A), account for the short duration of the reproductive period.

On exposed shores, but in the populations in the pools and in the sublittoral zone, although the main reproductive period is still October to early April (Text-fig. 7, no. 3*a*, *b*), it is more extended (June to April), as a very small percentage of the populations in these habitats bears reproductive tissue from June to September (Text-figs. 7, no. 3*a*, *b*; 8B). The extension of the reproductive period of the populations growing in these habitats is due partly to the persistence of small numbers of early summer sporophytes in the pools and of small numbers of summer and autumn sporophytes in the sublittoral zone (Table III) that first reach maturity during the summer and autumn following their germination; it is due equally to the retention of frond tissue in at least the sixth month of growth by a small percentage of the second-year spring plants (Table VIII; Text-fig. 8B).

In this species the reproductive period is longest in populations growing on sheltered parts of the coast in both intertidal and sublittoral-zone habitats. Here it extends usually from the middle or end of May until the beginning or middle of April (Text-figs. 7, nos. 4, 5; 9), but sometimes plants can be found bearing reproductive tissue during late April and early May (Text-fig. 7, no. 1). The percentage of plants bearing reproductive tissue is also much higher in these habitats from June to September than on exposed shores, although the period of maximum reproduction still occurs at the same time (Text-fig. 7, nos. 1, 4 and 5).

The slower rate of casting of the distal frond tissue in the older plants in these habitats is partly responsible for the increase in the percentage reproduction during the summer and autumn months (Text-fig. 7, nos. 1, 4); equally important, however, is the persistence of large numbers of summer and autumn sporophytes that start to bear reproductive tissue during the summer and autumn following their germination (Table VII; Text-figs. 7, no. 5; 9), when they are approximately 1 year old.

In most populations of this species growing on the British coast reproductive tissue is not developed by the plants during late April and early May. Two factors are responsible for the absence of reproductive tissue during this period. In some populations, particularly in those growing on exposed shores, the distal frond tissue persisting on the plants during that period is not normally more than 5 months old and consequently it does not develop reproductive tissue (Text-figs. 7, nos. 2, 3; 8A, B). In other populations, usually those growing on sheltered parts of the coast, although distal frond tissue in the sixth month of growth may be present on the plants during that period, it is still expanding (secondary growth above the 10 cm. level) and therefore does not form reproductive tissue (Text-figs. 7, nos. 4, 5; 9).

The few plants of this species which do bear reproductive tissue during late April and early May have either retained distal frond tissue in the seventh month of growth, or have distal frond tissue in the sixth month of growth that has reached its full expansion and can therefore produce reproductive tissue.

As the peak of secondary growth above the 10 cm. level occurs a month earlier on the Devon coast (February, March) than on the Argyll coast (March, April), there is a higher percentage of plants bearing reproductive tissue during late April and early May on the Devon coast, in habitats in which the plants can retain sufficiently old frond tissue to reach maturity (Text-fig. 7, cf. no. 1 with nos. 4 and 5).

From the above information on the reproductive cycles of populations of this species growing in different habitats it should be possible to estimate the approximate duration of the reproductive period in any population of *L. saccharina* growing on the British coast.

The data that have been accumulated during this work seem to indicate that the development of reproductive tissue in plants of this species is controlled by some factor or factors within the frond tissue of the plant, not by factors external to the plant. Van Overbeck (1940) extracted an auxin from a member of the Laminariales, *Macrocystis pyrifera*, and produced evidence to show that in this species the auxin was a growth hormone. It would be of interest if chemical changes, or an alteration in a hormonal balance, could be traced within the frond tissue of *L. saccharina* over a period of 6 months from the time of formation of the tissue until the tissue approaches maturity in the sixth month of growth.

WEIGHT OF THE SPOROPHYTE

In the literature there is very little information on the quantities of the different *Laminaria* species growing on the coastline of any country. From a Russian survey in July 1931 (Meyer, 1933) the stock of the Laminariales in the White Sea was estimated at 1,500,000 metric tons.

At the same time Kireeva & Schapova (1933) showed that, on the Murman coast in Kolsky Fjord and off Kildin Island, the average weight of a *L. saccharina* plant and of a *L. saccharina* population varied in different regions, the plant from 140 to 470 g. and the population from 4·7 to 5·7 kg./m.^{2}

Tikhovskaya (1940), working on the seasonal variations in the productivity and photosynthesis of *L. saccharina*, calculated that the biomass of *L. saccharina* in the Dalne-Zelenety Bay of the Barents Sea amounts to 4000 metric tons/km.^{2} He found that in August the average weight of a *L. saccharina* plant was 613 g. and that the weight of the *L. saccharina* population varied from 2 to 8 kg./m.^{2}, the weight of the population decreasing gradually towards the shore line from the level of 0·2 m. (height of water level above 0 depth). He also states that with decrease in level below 0·2 m. the plant size increased while the number decreased. The quantity of another species, *L. japonica* Aresch., growing on the coast of the Japanese Sea near Cape Povorotny is given by Gail (1935) as 4000 metric tons/km.^{2}

In the last few years only has any estimation of the quantities of the Laminariales on the British coast been attempted. In 1942 Chapman (1944) made a rapid survey for the Ministry of Supply of the quantities of the Laminariales growing round the coasts of England and Scotland. At the present time a detailed survey of the *Laminaria* resources of the Scottish coast is being made by the Scottish Seaweed Research Association. The results already published (Walker, 1947) show that the average growth of the Laminariales on the sublittoral areas so far surveyed around Orkney (Scapa Flow and Bay of Firth) amounts to just under 4000 metric tons/km.^{2} as against the estimated figure of 1400 metric tons/km.^{2} for plant production in the English Channel down to 70 m. (Atkins, 1923).

Maximum Weight

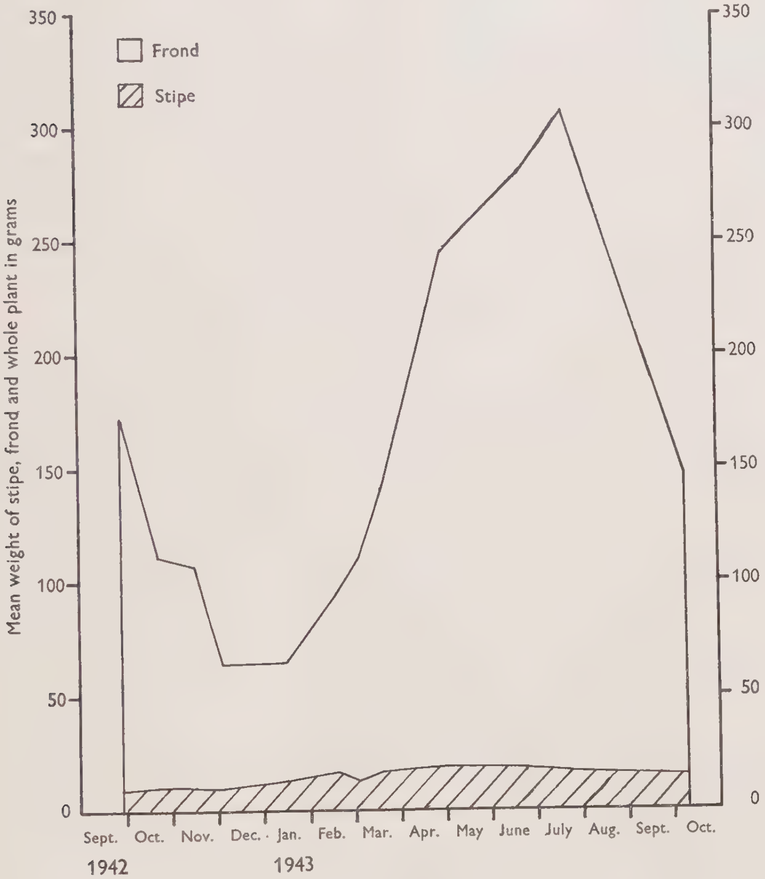
A plant of *L. saccharina* growing on the British coast reaches its maximum weight at the end of the second period of rapid growth when the frond tissue of the plant shows the greatest length and width. Winter- and spring-developed plants are eight to fourteen times heavier at the end of the second period of rapid growth than at the end of the first period of rapid growth; plants developed later in the year, however, do not show such a great difference in weight at the end of the two growth periods owing to the greater growth-rate during the first period of rapid growth. Depending on the bathymetric zone, habitat and geographical position in which the species is growing, the maximum weight of a plant can vary from 0·12 to 2·5 kg.

According to Yendo (1919) and Gail (1935) *L. japonica* and three other Japanese species also reach their maximum weight during the months of May and June in the second year of growth. They state, however, that these species perish after the second sporulation. Their life cycles are therefore similar to that of the *L. saccharina* plants growing in the intertidal zone on exposed parts of the British coast in habitats that dry out at low water of mean spring tides.

Seasonal Variation in Weight

On the British coast there is a seasonal variation in the weight of any *L. saccharina* plant (Text-fig. 10) whatever the age, bathymetric zone, habitat or latitude as there is in the frond size of the plant (Pls. V–VII, IX–XI). This seasonal variation in the weight of the sporophyte is also recorded by the

Russian workers for the White Sea and the Barents Sea. Kireeva & Schapova (1933, 1938) and Tikhovskaya (1940) show that on the Russian coast *L. saccharina* reaches its maximum weight in August and its minimum weight in March. On the British coast, however, *L. saccharina* reaches its maximum weight in June or July and its minimum weight in December or January (Text-fig. 10), that is, 1–2 months earlier than on the Russian coast. On the British coast the maximum weight is four to six times greater than the minimum weight, whilst on the Russian coast the maximum weight is recorded as seven times greater than the minimum weight (Kireeva & Schapova, 1938).



Text-fig. 10. Seasonal variation in the weight of *L. saccharina* plants growing on a raft in Plymouth Sound.

Variation in Weight with Bathymetric Zone, Habitat and Geographical Position

From the earlier sections of this paper it can be seen that the weight of any *L. saccharina* population depends on the bathymetric zone, habitat and geographical position in which the population is growing. With decrease in level on the shore down to 1–4 m. below E.L.W.S.T. the weight of a *L. saccharina* population increases, since the growth-rate of the plants increases and the depopulation-rate of the plants reaching their maximum weight usually decreases. For the same reasons there is also an increase in the weight of a population with the degree of shelter of a habitat, although the thickness of the frond tissue may decrease. The records show also that *L. saccharina* populations growing on the Argyll coast are heavier than the populations growing in similar habitats on the Devon coast, the increase in weight resulting from the more rapid growth of this species on the Argyll coast.

SUMMARY

The production, longevity, growth, regeneration and reproduction of *Laminaria saccharina* (L.) Lamour. on the Devon and Argyll coasts are described.

Bathymetric zone and habitat control the fertility and longevity of the gametophyte and consequently the production of the sporophyte. Sporophytes develop at the higher levels during the winter, early spring, late summer and autumn, and at the lower levels during spring, summer and autumn.

Longevity of the sporophyte depends on season of germination, bathymetric zone and habitat. Winter sporophytes rarely persist to maturity. Spring sporophytes form the bulk of all *L. saccharina* populations except on very sheltered coasts in the sublittoral zone where summer sporophytes may be equally numerous. On the British coast the life-span of a *L. saccharina* sporophyte does not exceed 3 years.

Growth of the sporophyte, although continuous throughout life, shows seasonal variation in rate, so that the yearly growth can be divided into two periods, one of more rapid growth (January to June) and one of slower growth (July to December). Seasonal change in rate of frond growth is indicated by change in shape of the base and also by the variation in the width of the tissue produced. The rate of growth of the tissue at successive levels up the frond also shows a seasonal variation. Seasonal change in rate of stipe growth is indicated by alternate zones or 'rings' of lighter and darker tissue, the darker being formed during the periods of slow growth. The approximate age of the sporophyte can be assessed from an examination of the holdfast.

The growth-rate changes with the increase in the age of the sporophyte, the maximum rate being reached during the second period of rapid growth. The

rate of growth also varies with change in bathymetric zone, habitat and latitude.

Distal frond tissue is cast continuously throughout the life of a sporophyte, the rate of casting varying with the time of germination and with the habitat. The normal age of the oldest frond tissue is from 5 to 7 months; 9-months-old frond tissue has not been recorded.

Complete regeneration of the frond after cutting occurs only in sporophytes up to the age of 1 year. No regeneration occurs when the whole frond is removed.

Sporophytes first reach maturity when they are from 8 to 12 months old.

For reproductive tissue to develop on a plant the distal tissue present on the frond must be in at least the sixth month of growth. Once reproductive tissue is present on frond tissue in the sixth month of growth, it can arise on frond tissue in the fifth month of growth but not on younger frond tissue.

The percentage of reproducing plants and the duration of the reproductive period in a population depend on the numbers of different season and year groups making up the population and on the habitat in which it is growing.

The maximum weight of the sporophyte is reached at the end of the second period of rapid growth. The sporophyte shows a seasonal variation in weight and also a variation in weight with change in bathymetric zone, habitat and geographical position.

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LUMBRICILLUS REYNOLDSONI N.SP., AN ENCHYTRAEID FROM THE BEACHES OF NORTH WALES

By Helge O. Backlund

Zoological Institution, Lund, Sweden

(Plate XIV and Text-figs. 1–4)

Dr T. B. Reynoldson of the Department of Zoology, University College of North Wales, Bangor, found some large enchytraeids on the shores of the Menai Straits. He suspected that it was an undescribed, or at least a rare and interesting species, and kindly sent six specimens to me for further study. I find that the specimens are indeed to be ascribed to a new species, which is here named *Lumbricillus reynoldsoni*, in recognition of the finder's prominent work on the ecology of *Lumbricillus lineatus* Mull. and *Enchytraeus albidus* Henle.

Dr Reynoldson gives the following description of the habitat. 'The worm was found in considerable numbers among decaying seaweed and the underlying gravel at the extreme high tide level along with *Enchytraeus albidus* Henle in the Bangor area of the Menai Straits at the locality known as Gorad-y-Gyt. It occurs all the year round here, and cocoons have been collected during March and April. So far these worms have not been taken from other shores in North Wales although search has been made during general collecting trips.'

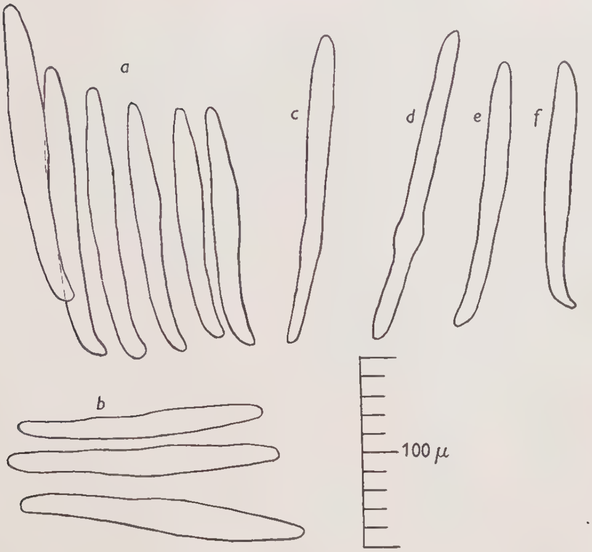
The specimens were excellently preserved. Dr Reynoldson had narcotized them with chloroform vapour and fixed them in Bouin's solution. Three specimens were examined in sections stained with Masson's and Mallory's stain respectively, one specimen was heated in lactic acid.

The length of the mature worm is 40 mm., the width 1·2 mm. The number of somites is about 65. The worm is opaque and light pink from the coloured blood. The segmental grooves are obsolete, while the clitellum is not prominent. The worm tapers at the hinder extremity. The prostomium is small and rounded. The head-pore is situated between pro- and peristomium. The mouth-grooves are shallow on the prostomium, deeper on the peristomium.

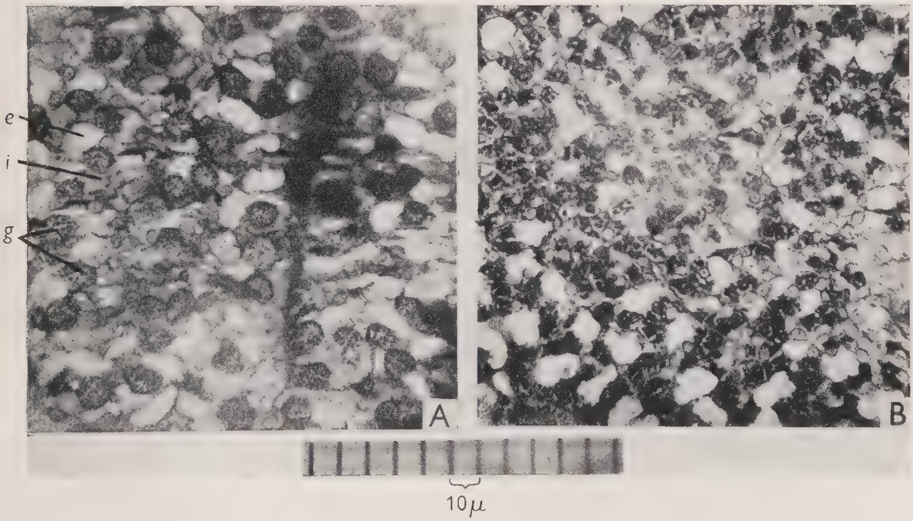
The setae (Text-fig. 1) are almost straight, particularly in the anteclitellar somites. The recently formed setae in the last somites are slightly smaller than the older ones. In the first 25–30 somites there are 5–*6*–7 lateral and 6–*8*–9 ventral setae, then the number decreases to 3–4 lateral and 3–4 ventral setae.

The cuticle is very thin for such a large species, only 1–1·2μ thick.

In the hypodermis there are no regular rows of enlarged gland cells. Instead, the whole hypodermis is scattered with small gland cells (Text-fig. 2A and Plate XIV, fig. 6). In their most active stage these cells are swollen and



Text-fig. 1. Setae (*a*) from somite 25, (*b*) from somite 60, (*c–f*) from various somites.



Text-fig. 2. A. Tangential section through hypodermis of anteclitellar somites; *e*, emptied gland cell; *i*, group of interstitial cells; *g*, active gland cells. The dark stripe is part of a muscle band. Masson stain. Red filter. B. Tangential section through clitellar hypodermis. Stain, filter and magnification as in A. The active gland cells are narrow, columnar. The mucous droplets much larger than in common gland cells.

almost spherical. They are then packed with mucous droplets which stain with aniline blue or with light green. Because of the pressure within the cell the nucleus, which is situated at the base, is usually seen protruding beyond the general cell surface. The formation of the mucus begins in cells of regular columnar shape, where it may be only slightly stainable. When the gland cells are emptied of the stainable mucus they remain swollen and are filled with small, diffuse chromophobic granules or droplets. The gland cells are most numerous in the prostomium and the anterior somites.

The clitellum covers half of somite 11, the whole of 12, and almost the whole of somite 13. It is saddle-shaped. The gland-free surface is, however, only a narrow ventral groove. There is no sharp border between the clitellar hypodermis and the normal hypodermis. The latter changes gradually into the former. The clitellar gland cells are scattered quite irregularly (Text-fig. 2B), often several gland cells are united into a group. These cells appear as irregular polygones in tangential sections. Their diameter is 5–9μ only. The height of the clitellar cells is approximately 50μ. Thus the gland cells are high and narrow, tapering at both ends. The nucleus is always at the narrow base of the cell and has a distinct nucleolus, but the rest of the chromatic matter is less distinct than in the interstitial cells. Instead, the nucleoplasm stains with iron trioxyhaematin. The mucous droplets are large, with a diameter of 1μ. They stain very brightly with light green, less so with aniline blue. The droplets are sharply defined, since the rest of the plasma remains unstained. The emptied cells lose their connexion with the basement membrane and become subspherical. They are situated just under the cuticle. These cells are not really quite empty, since they contain some unstainable, slightly granular matter. Their nuclei have no nucleolus and are little stained. In the narrow interstitial cells the nuclei may be situated at any level, but are usually concentrated near the basement membrane.

The muscle layers are thick. The circular muscles are well-defined bands which protrude into the hypodermis, giving the latter a wavy inner surface. The longitudinal muscles are of an extreme lumbricilline type, long and pointed. In transverse sections the longitudinal muscle bands are almost feathery and show a superficial similarity to those of *Lumbricus.*

EXPLANATION OF PLATE XIV

Fig. 1. Ectal duct of spermatheca with gland cells and muscles. Masson; red filter.

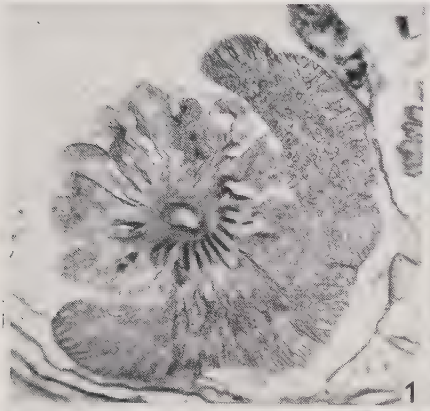
Fig. 2. Orifice of ectal duct into ampulla. Mallory; green filter.

Fig. 3. Ampulla with muscles and peritoneum. *b* blood vessel, *l* lymphocytes, *s* septal gland. Masson; red filter.

Fig. 4. Ampulla, ental duct and oesophagus. In the oesophagus a section through *Anoplophrya* sp. Mallory; green filter.

Fig. 5. Copulatory gland from somite 14. Mallory; green filter.

Fig. 6. Hypodermis with sporozoite in enlarged cell. Masson; red filter.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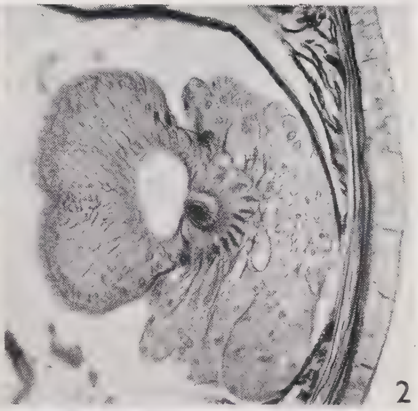
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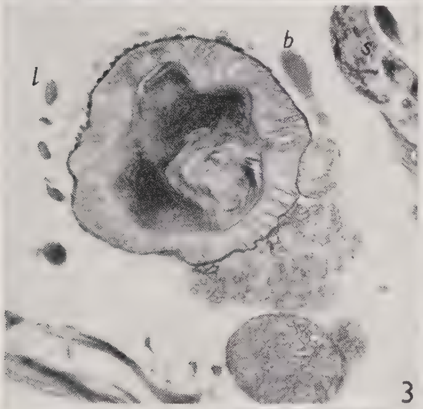

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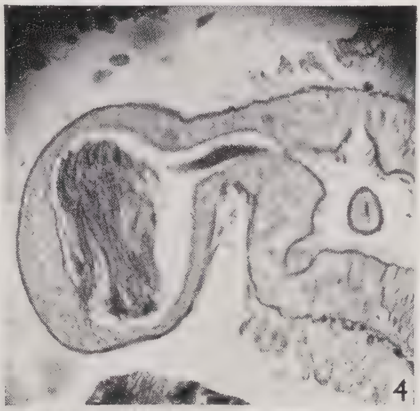
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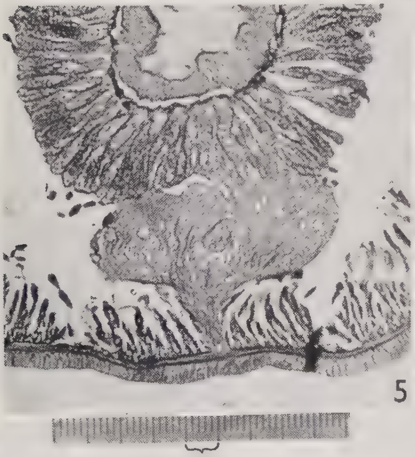

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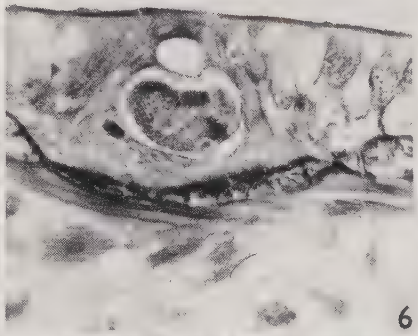


6

The peritoneum is highly developed. In many places it consists of several layers of loosely connected, slightly stainable cells and is rather reminiscent of some kind of parenchyma.

The lymphocytes are typical for the genus *Lumbricillus*. The numerous granulocytes are spindle-shaped or ellipsoidal with more or less pointed ends. One end often tapers into a delicate protoplasmic thread, which sometimes is attached to the peritoneum. The cells are filled with minute granules, which stain dark blue-violet in Mallory's, green in Masson's stain. In the spherical nuclei no nucleoli were observed. Aggregations of 5–10 rather small amoebocytes with inclusions of varying size are rather numerous.

There are no peptonephridia or other appendages or widenings of the intestine. The mouth-ridge is large and sharp, the bulbous pharynx is comparatively low. The intestinal epithelium shows several differentiations, but these are too insignificant to have any taxonomic value.

Septal glands occur in segments 4/5 to 6/7; that in 5/6 is the largest. Only the first two pairs fuse in the dorsal line. On the ducts from the glands in 5/6 and 6/7 there are proliferations of glandular tissue, but no real secondary glands.

Chloragogen cells begin in somite 4, but are again missing where the septal glands are at their largest. The chloragogen layer is dense, consisting of long, club-shaped sac-cells, which are only attached to the basement membrane by a narrow stalk (Pl. XIV, fig. 5). Naturally their length varies and reaches 200μ. The maximum width (at the tip) is 20μ. The long stalks contain but few chloragogen granules: most of these are concentrated in the sac-like body of the cell. The granules are small, not exceeding 1μ. They are arranged in a network around and between vacuoles of varying size, up to 12μ in diameter. Probably these vacuoles were filled with fat in the living specimens. The chloragogen granules retain their own yellow-brown colour and stain additionally with iron trioxyhaematin, the surrounding plasma stains slightly with light green. With Mallory's stain the chloragogen material in the body of the cells becomes bright red from acid fuchsin, whereas the small chloragogen granules in the cell stalks are yellow—probably their own natural colour. In the twelfth somite the chloragogen cells are missing; the intestine is covered only with a loose peritoneum of the same kind as on the body walls. Transitional stages between chloragogen cells and peritoneal cells occur.

The brain is 250μ long, 115μ high, and 185μ broad. Its anterior end is convex, the posterior end concave. The first ventral ganglion is large and protrudes in front of the brain connectives.

The first nephridium is situated in segment 6/7. The anteseptalium is small, consisting of the funnel only. The postseptalium is continuous with the terminal ectal duct.

The dorsal blood vessel originates in 14/15. It is enlarged in 14 and 13 and contains here nuclei belonging to a syncytium which is little stainable.

The testes are large, and much lobed. The sperm funnel is slightly bent. It is 750μ long and 280μ wide. The duct is central, 30μ wide. The collar is large but not so wide as the body of the funnel, 200μ only. It is not reflected. The distal end of the sperm funnel is square. The sperm duct is narrow. It is loosely and irregularly coiled and does not extend farther caudad than the penial bulb.

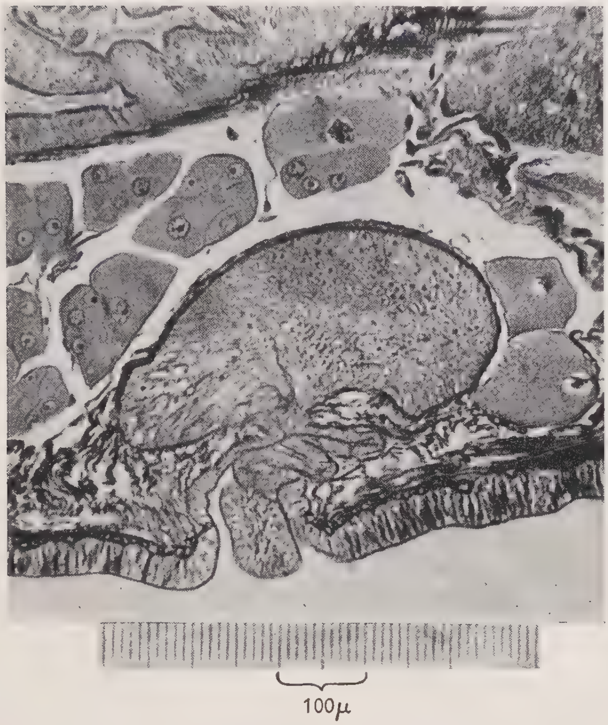
The penial bulb (Text-fig. 3) is strictly lumbricilline, large and covered with a thick muscular coating. It contains a large number of glandular cells in several layers. The penial invagination is very deep and much puckered. The oocytes are confined to somite 12.

The spermatheca (Text-fig. 4; Pl. XIV, figs. 1–4) consists of ectal duct, ampulla, and ental duct. The ectal duct is 140μ long and slightly bent. The lumen is approximately 18μ wide and is bounded by a cuticle which is thicker than the cuticle of the body surface. The walls of the duct consist of long and narrow gland cells. The length of the gland cells may be more than 150μ. In the proximal part, around the duct, there are naturally no intercellular spaces between these gland cells. But distally the cells are united into lobes of some 10–15 cells, the lobes being free from each other. The longest cells are club-shaped, with a narrow proximal neck. Not all gland cells reach the lumen of the duct, some are restricted to the distal parts of the lobes. However, these cells also have narrow extensions, forming ductules, to the cuticle of the duct. These ductules are exceedingly narrow and are visible only as darkly stained, wavy striations (like the ductules in the penial bulb). All nuclei are situated in the distal parts of the cells. The cells stain very lightly while the secreted granules are very small and scarce.

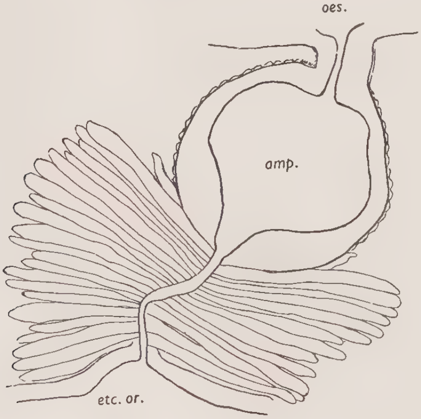
The subspherical ampulla is sharply defined from both the ectal and the ental duct. The length of the ampulla is approximately 290μ, the width 240μ. The walls are 30μ thick in the proximal, 12μ in the distal parts of the ampulla. Thus the lumen is pear-shaped. The cells are non-glandular, columnar in the proximal, cubic in the distal parts. Near the entrance of the ectal duct the inner surface is covered by a thick cuticle, but in the distal parts the inner surface of the ampulla is quite uncovered.

The ental duct is short, only 55μ long and there is a quite wide communication between ampulla and oesophagus. The lumen of the duct is 26μ wide, the total width is 50–55μ. The walls of the ental duct are similar to those in the distal part of the ampulla. In the innermost part of the ental duct the epithelium is ciliated as in the oesophagus.

The spermatheca has a rather interesting and complicated muscle-coating. At the ectal orifice muscles from the circular muscle layer are bent inwards. These muscles follow the ectal duct longitudinally. The muscle bands are broad in the radial direction, flat in the tangential. Thus, in perpendicular sections, the muscles appear as beams radiating from the lumen. The muscles are situated neither on the surface of the gland, nor in the innermost parts near



Text-fig. 3. Sagittal section showing penial bulb with deep invagination and oocytes. Intestine in the upper left corner. Mallory stain. Green filter.



Text-fig. 4. Outline of spermatheca. Schematic drawing with camera lucida.

the cuticle, but between the glandular lobes at the middle of their length. Often the thin parts of the muscles follow the walls of the gland cells closely. Therefore it may be hard to distinguish them from cellular surface-fibrillae. The muscles are continuous with the strong muscles which cover the ampulla. Here these muscles have again the same appearance as the sub-hypodermal circular muscles; they are, however, naturally weaker. On the ental duct the muscles become still weaker, similar to, and continuous with the muscles on the oesophagus. The peritoneal covering is very thin and probably incomplete on the glands of the ectal duct, but quite thick on the ampulla (Pl. XIV, fig. 3).

The elaborate muscle-coating of the spermatheca is a result of the structure of the ectal duct. Naturally, a duct with only glandular instead of epithelial walls must be supported by fibres when it is as large as in *L. reynoldsoni*. Since the fibres of connective tissue do not occur in enchytraeids the spermatheca is strengthened by muscles. I do not think that the muscles function in the emptying of the gland, but probably they do function when sperm is being ejected.

Large copulatory glands exist in somites 14 and 15 (Pl. XIV, fig. 5). The anterior and posterior ends are entirely free, but the median part surrounds the whole ventral nerve cord.

The specimens subjected to me were heavily parasitized. The intestine contained both infusorians, *Anoplophrya* sp. (Pl. XIV, fig. 4), and sporozoans in great numbers. The hypodermis of the prostomium and the first 35 somites held many, irregularly scattered, intracellular sporozoites (Pl. XIV, fig. 6).

Systematic position. Although this new species has almost straight setae it should without doubt belong to the genus *Lumbricillus*.[1] Its main character is the absence of peptonephridia. On account of the lobed testes the species should be placed in the subgenus *Lumbricillus* (= *Pachydrilus*). This subgenus inhabits mainly shore biotopes.

The full name of the new species is thus *Lumbricillus* (*Lumbricillus*) *reynoldsoni*.

The taxonomy of the subgenus *Lumbricillus* is rather complicated. *L. reynoldsoni* is, however, easily distinguished from all earlier described species. It is outstandingly large and the combination of characters of setae, spermatheca and copulatory glands do not occur elsewhere. This species has many characters in common with *L. pagenstecheri* (Ratz.), but the differences are easily seen from the diagnosis.

[1] On the authority of Dr Černosvitov I have earlier (Swedish Enchytraeida I and II, *Lunds Univ. Arsskrift* N.F. XLII, 13 and XLIII, 8) used the generic name *Pachydrilus*. On the suggestion of Dr Reynoldson I have looked through the older literature but could not find out why Černosvitov used the more recent name *Pachydrilus* Claparède 1889 instead of *Lumbricillus* Orsted 1861. Probably Černosvitov in his turn has followed his eminent compatriot Vejdovsky.

Diagnosis. Length 40 mm. Somites about 65. Blood pink. Clitellum saddle-shaped, not prominent, with small, irregularly scattered gland cells. Setae almost straight, L 5–7, V 6–9. Posterior end of brain concave. Nephridia with anteseptalium consisting of funnel only, with terminal ectal duct. Origin of dorsal blood vessel in 14/15. Penial bulb lumbricilline, with deeply puckered invagination. Spermatheca with subspherical ampulla sharply defined from both ectal and ental ducts. Ectal duct consists of large gland cells. Copulatory glands in 14 and 15 surround ventral nerve cord.

The type specimen (longitudinally sectioned) is in the author's collection at the Zoological Institution of Lund.

ON THE SEASONAL ABUNDANCE OF YOUNG FISH. IX. THE YEAR 1947

By P. G. Corbin, B.A.

Zoologist at the Plymouth Laboratory

(Text-figs. 1–3)

The 1947 records of the seasonal abundance of the pelagic young stages of teleosteans in the plankton of Plymouth off-shore waters are a continuation of the series of observations made by Mr F. S. Russell (1930–47). The form of the previous reports is retained. The dates on which collections were made are given in Table I, and the monthly average catches of young fish in Table II. The fortnightly averages of all young fish less clupeids are shown in Fig. 1, together with the corresponding curve for the period 1930–34.

1947 was the first year since the war in which collections were made throughout the twelve months. It is relevant, therefore, to relate the 1947 records to the interrupted observations of the years 1939 and 1946. Describing the conditions of 1939, Russell (1940) states that '...the year 1939 has been the worst yet recorded and sets a new low limit to the production of fish'. As a result of the break in observations due to the war, he says '...we may never know what point the trough of the decline may reach'. Reporting on the 1946 records after the resumption of observations, he writes 'The 1946 collections were started too late to include the main period of abundance of young fish resulting from the spring spawners, but they afford evidence that as regards the summer spawners at any rate there is no significant change from the conditions existing in 1939. We cannot say what the conditions have been during the intervening years, but analyses of phosphorus content of the water during each winter in the period 1939–46 tend to show that conditions have remained much the same as they are at present, and that it is unlikely that there has been any large incursion of rich water characterized by *Sagitta elegans* which supports a large population of young fish.' (Russell, 1947.)

In 1947, the total of all species of young fish was the lowest recorded since the observations started. All summer spawners were extremely scarce. Spring spawners were present in only slightly greater numbers, occurring mainly in two very small peaks in the second half of February and the second half of May. *Gadus luscus* and *Chirolophis galerita* contributed chiefly to the February peak, while the May peak was largely due to *Gadus merlangus* and *Callionymus* spp. It is of interest to record the occurrence of small numbers of young plaice, *Pleuronectes platessa*, in February. The young stages of this species were first taken in the Plymouth collections, also in small numbers, in

TABLE I. DATES ON WHICH COLLECTIONS WERE MADE, 1947

All 2 miles east of Eddystone, unless otherwise stated

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
29	2	6	3	23	2	7	11	1	6	13	3
..	10	12	8	27	16	14	18	10	13	19	10*
..	17	17	17	29	24	22	25	29	21	25	19
..	27	..	25	..	..	28	..	..	27	..	22
..	..	..	..	..	..	..	..	..	..	..	29

* Station E 1.

TABLE II. MONTHLY AVERAGE CATCHES OF POST-LARVAE PER HALF-HOUR
Oblique hauls with 2 m. ring-trawl, 1947

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Total young fish	..	42	76	27	65	35	19	46	27	62	7	5	411
Ditto, less Clupeids	..	24	8	7	54	25	7	15	6	1	1	+	148
All Clupeid spp.	..	18	67	20	11	10	12	32	21	60	7	5	263
Clupea harengus	..	..	..	..	..	..	..	..	..	..	..	..	..
Gadus pollachius	..	..	..	1	+	..	..	..	..	..	..	..	1
Gadus merlangus	..	..	..	1	22	6	1	..	..	..	..	..	30
Gadus minutus	..	..	2	1	2	..	..	..	..	..	..	..	5
Gadus luscus	..	9	1	..	..	..	..	..	..	..	1	+	11
Gadus callarius	..	..	..	..	..	..	..	..	..	..	..	..	..
Onos spp.	..	..	..	+	3	13	1	..	..	..	..	..	17
Molva molva	..	..	..	..	+	..	..	..	..	..	..	..	+
Merluccius merluccius	..	+	..	..	..	..	..	..	..	..	..	..	+
Raniceps raninus	..	..	..	..	..	..	..	+	..	..	..	..	+
Capros aper	..	..	..	..	..	..	..	..	..	..	..	..	..
Zeus faber	..	..	..	..	..	..	..	..	..	..	..	..	..
Arnoglossus spp.	..	..	..	..	..	..	..	1	1	+	..	..	2
Rhombus spp.	..	..	..	..	..	..	..	+	+	..	..	..	+
Scophthalmus norvegicus	..	..	..	..	5	..	..	..	..	..	..	..	5
Zeugopterus punctatus	..	..	..	..	2	..	..	..	..	..	..	..	2
Zeugopterus unimaculatus	..	..	..	..	..	..	..	..	..	..	..	..	..
Pleuronectes platessa	..	2	..	..	..	..	..	..	..	..	..	..	2
Pleuronectes limanda	..	..	..	..	4	1	..	..	..	..	..	..	5
Pleuronectes flesus	..	..	..	1	..	..	..	..	..	..	..	..	1
Pleuronectes microcephalus	..	..	..	..	1	..	..	..	..	..	..	..	1
Solea vulgaris	..	..	..	+	+	..	..	..	..	..	..	..	+
Solea variegata	..	..	..	..	1	..	..	..	..	..	..	..	1
Solea lascaris	..	..	..	..	..	..	..	+	..	..	..	..	+
Solea lutea	..	..	..	..	..	..	..	..	..	..	..	..	..
Serranus cabrilla	..	..	..	..	..	..	..	..	..	..	..	..	..
Caranx trachurus	..	..	..	..	..	..	..	1	2	..	..	..	3
Mullus surmulletus	..	..	..	..	..	..	..	..	..	..	..	..	..
Morone labrax	..	..	..	..	..	..	..	..	..	..	..	..	..
Ammodytes spp.	..	+	+	1	..	+	..	+	..	..	..	..	2
Ammodytes lanceolatus	..	+	..	..	2	2	+	..	..	..	..	..	4
Cepola rubescens	..	..	..	..	..	..	..	..	1	..	..	..	1
Callionymus spp.	..	..	..	..	11	3	1	4	1	+	..	..	20
Labrus bergylta	..	..	..	..	..	..	+	..	..	..	..	..	+
Labrus mixtus	..	..	..	..	..	..	..	..	..	..	..	..	..
Ctenolabrus rupestris	..	..	..	..	..	..	1	2	+	..	..	..	3
Crenilabrus melops	..	..	..	..	..	..	..	..	..	..	..	..	..
Centrolabrus exoletus	..	..	..	..	..	..	..	..	..	..	..	..	..
Trachinus vipera	..	..	..	..	..	..	..	+	..	+	..	..	+
Scomber scombrus	..	..	..	..	..	..	..	3	+	..	..	..	3
Gobius spp.	..	..	..	..	..	..	..	..	..	..	..	..	..
Lebetus scorpioides	..	..	..	..	..	..	..	..	..	..	..	..	..
Blennius ocellaris	..	..	..	..	..	..	..	..	..	..	..	..	..
Blennius pholis	..	..	..	..	..	..	+	+	+	..	..	..	1
Blennius gattorugine	..	..	..	..	..	..	2	2	1	..	..	..	5
Chirolophis galerita	..	12	4	..	..	..	..	..	..	..	..	..	16
Agonus cataphractus	..	..	..	..	..	..	..	..	..	..	..	..	..
Trigla spp.	..	..	..	..	..	..	..	+	..	+	..	..	+
Cottus spp.	..	..	..	1	..	..	..	..	..	..	..	..	1
Liparis montagui	..	..	..	..	+	..	..	..	..	..	..	..	+
Lepadogaster bimaculatus	..	..	..	..	..	..	..	..	..	..	..	..	..
Lophius piscatorius	..	..	..	..	..	..	..	..	..	..	..	..	..
Pipe fish	..	..	..	..	..	..	..	..	..	..	..	..	..

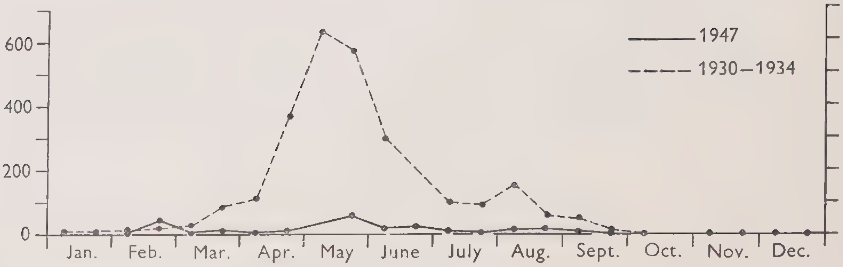


Fig. 1. Curves showing the average catches in half-hour oblique hauls with the 2 m. stramin ring-trawl for each fortnight for all young fish, excluding clupeids, in 1947 (————), and the same average over the period 1930–34 inclusive (– – – –).

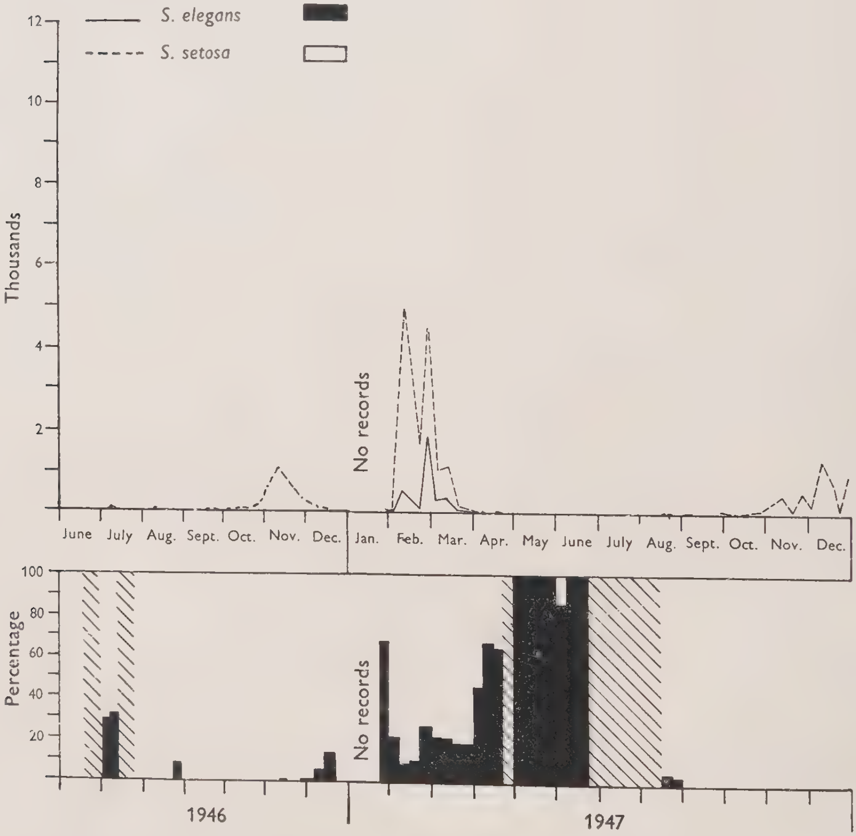


Fig. 2. Above, curves showing the actual abundance of *Sagitta elegans* (————) and *S. setosa* (– – – –) in half-hour oblique hauls with the 2 m. stramin ring-trawl during the period June 1946 to December 1947. Below, the percentage composition of the *Sagitta* populations during the same period: *S. elegans*, black; *S. setosa*, white; no *Sagitta*, hatched. (Continued from Russell, 1947, p. 607, fig. 2.)

February and March, 1939 (Russell, 1940). Since then this low incidence has evidently been maintained in the area. None was, however, recorded in 1946, as collecting was not resumed until June, well after the end of the spawning season of the plaice. The 1947 total (1403) of all species of young fish for the whole year was only 16% greater than the 1946 total (1203) for the seven months period, June to December. It is only too evident that the decline in production of young fish continues without sign of recovery thus fully bearing out the observations of the incomplete year of 1946 and the deductions from the 1939–46 winter phosphate data.

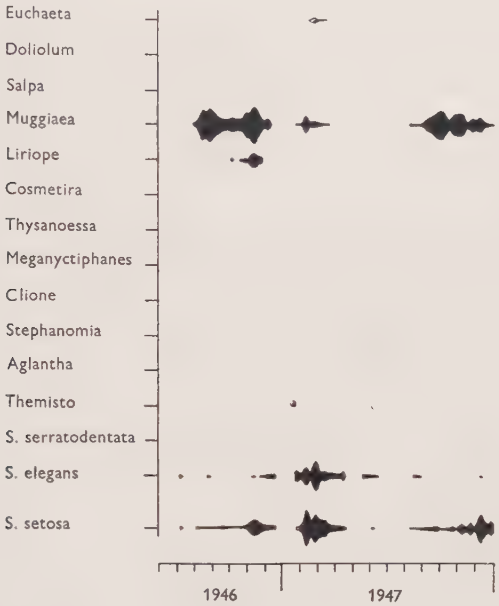


Fig. 3. Diagram showing the occurrence of the various plankton indicators in the collections off Plymouth during the period June 1946 to December 1947. The *Muggiaea* were all *M. atlantica* with the exception of a very few *M. kochi*, generally less than 1%, which occurred during August and September, 1946. (Continued from Russell, 1947, p. 607, fig. 3.)

Plankton indicator species (Figs. 2, 3) showed no great change from the conditions of 1946 when there was a notable scarcity of plankton organisms. *Sagitta setosa*, although never numerous and almost completely absent during May–July, generally predominated over *S. elegans*. The high proportion of *S. elegans* in May and June (lower part of Fig. 2) was not in fact due to large catches of this species (upper part of Fig. 2); the maximum haul during this period contained only 17 specimens of *S. elegans*. In April the numbers of both species of *Sagitta* were similarly very low.

Dr L. H. N. Cooper has kindly provided the information that phosphate values remained poor throughout the year. Towards the end of February, however, there was evidence of some richer water in the neighbourhood; the values at Eddystone were noticeably higher than those at E 1, 10 miles farther out, and the plankton catch was also richer.

Muggiaea atlantica was present in considerable though not exceptional numbers from January to March, and again from August to December; it was absent from April to July. *M. kochi*, which was present in small numbers in 1946 (Russell, 1947), did not occur in 1947.

Mr Russell wishes to correct an error which occurred in this latter paper; *M. atlantica* has been dominant since the winter of 1936, and not 1926 as given. The sequence of dominant species over past years is here summarized:

M. atlantica	1913–1924
M. kochi	1925–1936
M. atlantica	1936–1947

A few *Euchaeta hebes* were recorded in the early part of the year: February 17 (2), 27 (19); March 6 (3), 12 (1). Small numbers of Euphausian larvae occurred in January, February, April, June, August and November.

Pilchard eggs were numerous during the year. The following catches were made: April 25 (960); May 23 (405), 27 (10,200), 29 (12,700); June 2 (6450), 16 (14,650), 24 (28,950); July 7 (15,000), 14 (4600), 22 (4750), 28 (43); August 11 (580), 18 (140), 25 (45); September 1 (41), 10 (680), 29 (65); October 6 (172), 13 (650), 21 (53), 27 (2); November 13 (1), 25 (4); December 10 (5), 22 (4).

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THE RELATION OF THE SUBSTRATUM TO THE METAMORPHOSIS OF *OPHELIA* LARVAE

By Douglas P. Wilson, M.Sc., F.R.P.S.

Zoologist at the Plymouth Laboratory

(Plates XV–XVII)

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INTRODUCTION

It has previously been shown for the pelagic larvae of more than one species of polychaete (Wilson, 1932, 1937; Day & Wilson, 1934) that there is a period of time varying from a few days to several weeks during which the fully developed larva will metamorphose whenever it comes into contact with a substratum suitable for adult life. During this period the larva is able to test the varying types of bottom over which the currents carry it and to select and metamorphose in the particular kind of mud, sand or gravel that forms the normal habitat of the species. The natural processes of development thus do not force metamorphosis to take place at some definite critical stage in the growth of the larva. It is the external environment, or some feature of it, which stimulates the larva to change from an active free-swimming organism to a sluggish semi-sedentary worm buried in the bottom.

The power of selection is likely to be most strongly developed in species restricted to particular kinds of bottom soil. It would obviously not be so important to a species capable of inhabiting a wide range of bottoms, but would be an invaluable factor in aiding the survival of those confined to one special kind of sand or mud. *Ophelia bicornis* Savigny is such a species; it appears to be confined to loose, clean sand in which few other animals are present. It is abundant in certain parts of the Exe estuary, notably on the Bullhill Bank and the Polesands, where it has flourished since at least the beginning of the century, Allen & Todd (1902) having found it in large numbers in the same locality nearly fifty years ago. For a chart of the locality reference should be made to their paper. The development of this species is described separately (Wilson, 1948). In this paper are recorded the results of experiments designed to test the assumption that the larvae would exhibit a marked preference for sand from the adult habitat and would not readily undergo metamorphosis if other sands, or none at all, were supplied. This having proved true, later experiments were devoted to an attempt to discover how the larvae distinguish between various kinds of sand and to show that actual selection can take place, to some extent at least, in the unnatural confines of a glass dish. *Ophelia* larvae proved very suitable on the whole for experiments of this nature. Apart from their strongly marked reaction to various kinds of bottom they live well crowded in small dishes, and it appears unnecessary to supply food, for though some flagellates were added occasionally their presence does not seem to have made any difference. They are ready to metamorphose within the fortnight, a great advantage over larvae requiring a long rearing period before being ready to settle, and they are just large enough for the main features of the metamorphosis to be visible with a high-power dissecting binocular. The photomicrographs by electronic flash reproduced in Plate XV, figs. 1–3, give a fairly good impression of the appearance of the various stages alive among sand grains from the Bullhill Bank. Ideally the larvae should be just a little larger, as they are undoubtedly difficult to find in most sands until they move. When sand is first removed from an experimental dish, and strewn underwater in a glass tray for searching, the metamorphosed young worms curl up and tend to keep still for a time. After some minutes they begin to crawl about again, and it is then that they are most easily found. Moreover, being smaller than many of the sand grains they are often concealed from view unless active. Their chief drawback is their power of adhesion, strongly developed in the later stages, which causes them to stick to the surface film, to glass, to cotton fragments (Plate XV, fig. 4) and other debris, and to one another by the mucus they secrete. At first they pull themselves free, but later on are unable to do so in the quiet water of a dish. The practical difficulty of supplying some substitute for the strong currents of their natural environment was not overcome in these experiments.

Worms were collected and fertilizations made as have already been described in another paper (Wilson, 1948). The methods adopted will be described under each experiment.

The Preliminary Experiments of 1946

Experiment 1

The results of an early experiment to compare the reactions of larvae in the presence of sand to larvae kept in clean dishes are shown in Table I. Two finger bowls, each containing numerous larvae from the same fertilization, were stood side by side so that as far as possible each was under the same conditions of lighting and temperature. To one bowl sand from the Polesands was added. The water in the bowls was unfiltered outside sea water, and it contained numbers of small diatoms, flagellates, etc. Little attention was paid to this preliminary experiment, because during the period that it was running the main embryological features of the development were being worked out, but the bowls were examined from time to time. It will be seen that larvae in the bowl with sand soon metamorphosed, whilst the great majority in the clean bowl did not do so. On 6 May the newly metamorphosed worms were crawling actively among the sand grains and seemed particularly healthy in comparison with the unmetamorphosed larvae and the few partially metamorphosed ones sticking to the bottom of the clean bowl. Conditions were similar on 13 May. Owing to pressure of other work these bowls were not disturbed again until 6 June, when it was found, with some astonishment, that the clean bowl still contained many unmetamorphosed larvae which, although stuck to the bottom with the anal papillae, swam when released.

TABLE I. EXPERIMENT 1

(Begun 27. iv. 46 with larvae from a fertilization of 18. iv. 46.)

	Clean bowl	Dish containing Polesand sand	Polesand sand
29. iv. 46	Unmet.	—	? Meting
6. v. 46	Majority unmet.; a few have lost their prototrochal cilia	—	Majority metd
13. v. 46	Majority unmet.	—	All metd
6. vi. 46	Some dead, but many unmet. with strong prototrochs and often telotrochs. Some larvae removed to small dish containing sand	Unmet. larvae introduced from clean bowl	All metd
12. vi. 46	Many dead but living larvae still with prototrochs, teletrochs and sometimes apical tufts	Sand searched; found 21 metd or meting, 2 unmet. and 2 dead larvae	Not examined
5. vii. 46	All dead	All dead	All dead

The following contractions are used in tables: metd, metamorphosed; meting, metamorphosing; unmet. unmetamorphosed; *c*. approximately; *d*, dead.

There was considerable algal growth on the sides and bottom of the bowl testifying to its age, but the bowl was unusually healthy and there were no ciliates visible in spite of the remains of several dead larvae. The sand bowl, on the other hand, was much infected with ciliates, but in the sand there were numerous young worms with long bristles, although still only at the three-setiger stage beyond which none has so far been reared. On this date an uncounted number of unmetamorphosed larvae were removed from the clean bowl and placed in a smaller dish containing Polesand sand. Six days later a search of this sand revealed that the majority had metamorphosed or were metamorphosing, whilst in the clean bowl, in spite of many further deaths, there were still larvae with prototrochs, telotrochs and sometimes apical tufts. Thus, 7 weeks after fertilization, larvae were still able to swim and to metamorphose, given suitable sand conditions; this, although other larvae from the same fertilization had completely metamorphosed some 5 weeks previously.

There is no doubt that the larvae fertilized on 18 April 1946 were one of the healthiest cultures I have had. They were much used in working out the details of the development and in making the drawings published in the previous paper (Wilson, 1948). I have not since been able to keep larvae unmetamorphosed and healthy over such a long period of time, but quite early in the work it was noted that the healthier the culture the more definite are the reactions of the larvae to the presence or absence of suitable sand. Unhealthy larvae are much more liable to start metamorphosing without sand; particularly do they lose cilia and become unable to swim. This fertilization of 18 April was, on 13 May, the subject of a special note contrasting its health most favourably with other cultures in being at that time. This fertilization was made from worms collected at Exmouth on 13 April and sent to Plymouth by rail.

Experiment 2

Sixty swimming larvae 9 days old were placed in each of three dishes, respectively the clean control, a dish with sand from the Bullhill Bank, and a dish with flocculent mud from Salcombe (Table II). On examination 5 days later only fifty-two larvae were found in the clean control, but fifty of them were unmetamorphosed. In the Bullhill sand twenty-four metamorphosed young worms were found together with seven unmetamorphosed and two dead, one of the latter possibly metamorphosed. In the mud, in spite of a careful search, protracted over 3 hr., only five larvae were accounted for and only one of them was metamorphosed. Three days later the remaining larvae in the clean control were still unmetamorphosed.

TABLE II. EXPERIMENT 2

(Begun 29. v. 46 with larvae from a fertilization of 20. v. 46.)

	Clean dish	Bullhill sand	Salcombe mud
29. v. 46	Unmet. 60	Unmet. 60	Unmet. 60
3. vi. 46	Metd 1 Unmet. 50, *d* 1	Metd 24 Unmet. 7, *d* 2	Metd 1 Meting 2 Unmet. 1, *d* 1
6. vi. 46	All unmet.	Not examined	Not examined

The discrepancy between the numbers of larvae put into each dish and the number found is easily explained. Nine-days-old larvae stick readily to any solid object, and very likely some of them were lost in the pipette and never got into the dishes at all. Too much sand and mud were used in this experiment, making it extremely difficult to carry out a complete search. Larvae are especially easily concealed in the mud, but, nevertheless, it seems highly probable that in the mud the majority were smothered and died.

The difficulty experienced in transferring known numbers of larvae from one dish to another, and more especially in finding them all again in even very small quantities of sand or mud, made it necessary to adopt a somewhat easier technique. It was thought that if a comparatively large, though unknown, number of larvae were put into each experimental dish, it would be sufficient for the purpose of the experiment to recover only a fraction of them. Any marked difference in reaction to various types of bottom deposits would be shown by the proportions of metamorphosed to metamorphosing and unmetamorphosed larvae among those recovered by random sampling. It would not be necessary to search the whole of the sands or mud; this would result in a great saving of time and labour. As it turned out even this method demanded a great expenditure of time and effort, and it was physically impossible for one person to do more than was done by working long hours whilst the experiments were in progress. The results, however, were on the whole satisfactory for the purpose in hand, and marked differences in settlement reactions to the various soils were clearly shown.

Experiment 3

This was the first of the experiments in which tests were made of a number of different types of bottom deposits. Small glass dishes approximately 3 cm. in diameter were thinly strewn with the deposits to be tested. The deposits were sterilized by boiling and well washed in filtered sea water before being used. The dishes were put all together on black paper on a large enamel tray, covered with glass covers and placed in a comparatively cool place. A considerable but unknown number of larvae were put into each. The larvae were 8 days old and were showing the first signs of settling. The experiment is summarized in Table III.

On 21 June, 8 days after the start of the experiment, none of the larvae in the clean dish had metamorphosed. They were attached by their anal papillae to the bottom of the dish, to the surface film, or to cotton fragments or other debris, sometimes in clusters. Almost all had prototrochs and telotrochs, but one or two were seen which had lost the cilia. When water was squirted at them with a pipette the larvae came off the bottom and swam about for a time. In contrast with this was the condition in the dish containing Bullhill sand (Pl. XVI, fig. 1); here, except for a few unmetamorphosed larvae on the surface film, the sand was alive with metamorphosed young worms with long bristles. In a few minutes thirty were counted, but there were many more. One unmetamorphosed and two metamorphosing larvae were also found. It was quite evident that the great majority of the larvae in this dish had metamorphosed, almost the only unmetamorphosed ones being stuck to the surface film. On the other hand, the dish with a few grains of Bullhill sand sprinkled over the bottom contained no metamorphosed larvae, though about 10% had lost or were losing the prototrochal cilia, generally the first stage in metamorphosis. The fine 'Gritty' sand (Pl. XVII, fig. 3) consisting of particles of an angular nature with sharp edges and corners had many larvae in or on it, but not one had metamorphosed, although sixteen had lost their prototrochal cilia and may have been beginning to metamorphose. A hundred unmetamorphosed larvae were actually counted and there were still more left in the sand. In the shell gravel a small proportion had metamorphosed and rather more were metamorphosing though a large majority were unmetamorphosed. The mud, as usual, was difficult to search, but in 2 hr. forty-seven unmetamorphosed larvae were seen. Four of these had lost the cilia of the prototroch, but it is doubtful whether they were actually metamorphosing. Not a single metamorphosed worm was found in this dish.

TABLE III. EXPERIMENT 3

(Begun 13. vi. 46 with larvae from a fertilization of 5. vi. 46.)

	21. vi. 46		2. vii. 46
Clean dish	Unmet. *c.* 150	—	Many dead. A few living unmet.
Bullhill sand	(a) Unmet. 10	(c) Metd 30 Meting 2 Unmet. 1	Good number metd, healthy. 1 or 2 unmet.
Bullhill sand (a few grains only)	(a) Unmet. 25	(c) Metd 0 Possibly meting 10 Unmet. 80–90	Mainly dead or dying, unmet. A few may be partially metd
Fine 'Gritty' sand	(a) Unmet. 12	(c) Metd 0 Meting 16 Unmet. 100	None properly metd, but a fair number possibly meting
Shell gravel	(a) Unmet. 6	(c) Metd 4 Meting 29 Unmet. 60	Several metd, a few meting and a few unmet. Some dead.
Salcombe mud	(a) Unmet. 4	(c) Metd 0 Meting 0 Unmet. 47	None seen

(a) on surface film; (c) in gravel, sand or mud.

After the examination on 21 June all the counted larvae and deposits were returned to their respective dishes. On 2 July a further, but briefer, examination was made. The results are summarized in Table III and do not need a detailed explanation.

This experiment shows clearly that larvae will settle readily in Bullhill Bank sand and there metamorphose at an age when they will scarcely do so at all in other deposits. The fact that larvae on the surface film only a little distance above the sand do not metamorphose at the same time as those in it seems to indicate that physical contact with the sand is the main stimulus to metamorphosis. A few thinly scattered and isolated grains of this sand are less effective in bringing about metamorphosis than a deposit of the coarser particles of shell gravel.

Experiment 4

In order to investigate more fully the relation between the physical character of the bottom deposit and metamorphosis a bigger experiment along similar lines to that of Exp. 3 was undertaken. Except for the omission of mud the same types of bottom were repeated with, in addition, several new natural and artificial deposits. Before the actual results set out in Table IV are considered these need some explanation.

Penrhyn Bay sand (Pl. XVII, fig. 1) came from a shore in north Wales where, to the best of my belief, *Ophelia* is absent. It is similar in many respects to Bullhill Bank sand (Pl. XVI, fig. 1), the grains generally being well rounded, though on the whole smaller (see analysis, p. 736), and it contains a considerably higher portion of shell fragments. Eddystone shell gravel consists mainly of relatively large and worn shell fragments; they were well washed so as to be much cleaner than they are in nature. The fine 'Gritty' sand has already been described. The other bottoms were more artificial in nature: Bullhill sand mixed with a roughly equal proportion by volume of well-washed Carborundum grit No. 120 (Pl. XVII, fig. 4); the Carborundum grit alone; Bullhill sand cemented in a single close layer to the bottom of a dish with Murrayite cement, so that each grain was immovably fastened by its base though in contact with neighbouring grains; fragments of broken No. 1 cover-glass; glass wool in a fairly thick layer on the bottom of the dish; fine capillary tubing broken up and in a heap; similarly with coarser tubing; finally, lattices made of criss-crossed strips of No. 1 cover-glass and rather thicker glass. The strips were crossed in layers at right angles and cemented together with Murrayite cement at the points of contact. The larvae could thus get in between the horizontal layers of glass separated by a distance equal to the thickness of the glass used. These thicknesses were: for No. 1 cover-glass about 180 μ; for the thin glass about 330 μ. The larvae used in this experiment came from a very successful fertilization made on 1 July. Almost 100% of the eggs developed and the larvae were very healthy. The experiment was started on 6 July at a time when all the larvae were swimming freely in their finger bowls. They were at a stage when the first two setigers have bristles, but those of the third setiger have not appeared. A large but unknown number of larvae were put into each of the small experimental dishes of approximately 3 cm. internal diameter. As before, these were all covered and stood together on black paper in a cool place not too strongly illuminated.

Two days later the dishes were examined as closely as possible without removing the deposits from the bottom. In almost every dish the great majority of the larvae were swimming actively, but in the dish with Bullhill sand few were swimming, and it was seen that the majority were in the sand metamorphosing or metamorphosed, the latter crawling actively among the sand grains. They already had the characteristic long bristles which none of

TABLE IV. EXPERIMENT 4

(Begun 6. vii. 46 with larvae from a fertilization of 1. vii. 46.)

	8. vii. 46	11. vii. 46			
Clean dish	Almost all swimming. A few stuck to bottom	Some swimming, majority sticking on surface film and bottom, all unmet.			Very healthy
Bullhill sand	A few swimming, but majority in sand meting and metd	(a) Metd 1 Meting 1 Unmet. 15	(b) None	(c) Metd 50+ Meting 0 Unmet. 4	Mainly very healthy
Penrhyn Bay sand	Majority swimming. A few in sand unmet.	(a) Unmet. 35	(b) 15 at least	(c) Metd 20, *d* 2 Meting 11, *d* 3 Unmet. 43, *d* 4	All living fairly healthy
Eddystone shell gravel	All swimming	(a) Unmet. 50	(b) A good number	(c) Metd 1 Unmet. many	Very healthy
Fine 'Gritty' sand	All swimming	(a) Unmet. 6	(b) 97 at least	(c) Metd 5 Meting 7 Unmet. 32	Healthy
Bullhill sand and Carborundum	Majority swimming. A few in mixture, one metd	(a) Unmet. 28	(b) 16	(c) Metd 3 Meting 6 Unmet. 67+	Very healthy
Carborundum	Majority swimming. None metd	(a) Unmet. *c.* 60	(b) 50+	(c) Many unmet.	Very healthy
Bullhill sand cemented in a single layer	1 or 2 swimming, others on surface film or in sand	(a) Unmet. 12	(b) 12	(c) Metd 1 Meting 0 Unmet. 56	Healthy
Broken cover-glass	Majority swimming. Some among fragments. A few metd	(a) Unmet. 7	(b) 4	(c) Metd 8 Meting 2 Unmet. 116	Healthy
Glass wool	1 or 2 swimming. Majority in wool unmet.	(a) Unmet. 10	(b) None	(c) Metd 4 Meting 1 Unmet. 68, *d* 2	Living larvae healthy
Broken fine capillary glass tubing	Majority swimming. Some amid tubing unmet.	(a) Unmet. 32	(b) 2 or 3	(c) Unmet. *c.* 100	Healthy
Broken coarse capillary glass tubing	Almost all swimming	(a) Unmet. 7	(b) None	(c) Unmet. *c.* 100	Healthy
Lattice of No. 1 cover-glass	Majority swimming. Some in lattice unmet.	(a) Unmet. *c.* 60	(b) 2 or 3	(c) All unmet. on bottom of dish or in and about lattice	Healthy
Lattice of thin micro-slide	Majority swimming, some in lattice unmet.	(a) Unmet. 60	(b) 2 or 3	(c) All unmet. on bottom of dish or in and about lattice	Healthy

(a) on surface film; (b) swimming freely; (c) in bottom deposit.

the swimming larvae possessed. Even in the cemented Bullhill sand the larvae were down amid the grains, though here only one larva was seen to be probably metamorphosing, all the others were unmetamorphosed. The glass-wool had attracted, or trapped, many but none was metamorphosed. Amid the broken cover-glass, however, there were a few metamorphosed larvae with long bristles crawling about, though the majority still swam. The difference between the Bullhill sand and the Penrhyn Bay sand was striking.

On the fifth day of the experiment each dish was carefully searched, the various deposits being removed for this purpose. The results are summarized in Table IV, but it should be noted that except for the clean dish, and the various deposits of glass where it was relatively easy to find all the larvae present, a complete count or examination of every larva in the dish could not for certain be made. However, in the half-hour and more devoted to each dish few larvae can have escaped observation. In the Table a + after a figure means that more larvae were seen than were actually counted.

In every dish larvae were trapped on the surface film, sometimes in quite large numbers. These must be ignored when comparing the effect of the different types of bottom, though a word must be said concerning the single metamorphosed and the metamorphosing larva on the film above the Bullhill sand. It is quite probable that these had been carried from the sand below by air bubbles such as are formed when gases come out of solution during a rise in temperature, or in photosynthesis. Indeed, on 11 July there were also grains of sand on the film; these had not been there previously and must have been raised in some such way. There were similar sand grains in the Penrhyn Bay dish and Carborundum grains on the surface film in the two dishes containing that substance. Indeed, the appearance of sand grains on the surface film is a not unusual feature during the course of an experiment, and the presence, therefore, of metamorphosed larvae on the film does not necessarily imply that they metamorphosed in that position. In this experiment there were large numbers of metamorphosed larvae in the Bullhill sand on 6 July, and as since that date sand grains had appeared on the film it is not surprising to find that one or two of these larvae had been carried up with them.

The results as set out in Table IV largely speak for themselves. Once again in the Bullhill sand dish the larvae are far ahead of all others in metamorphosis and in the development of long bristles. In the unmetamorphosed larvae the bristles were much shorter and those on the third setiger were on this same day only just protruding from the seta sacs—the young metamorphosed worms had third setiger bristles many times this length, and those of the first and second setiger were likewise elongated over those of their unmetamorphosed relatives. Penrhyn Bay sand had by this fifth day induced a fair proportion to metamorphose, but was definitely well behind Bullhill sand. A few metamorphosed worms with their long bristles were found in some of the other dishes, but the proportions are much smaller still. It is striking how the addition of Carborundum grit and the cementing of the grains in an immovable single layer each upsets the metamorphosis-inducing properties of the Bullhill sand.

Experiment 5

The results of the preceding experiments having indicated that the stimulus to metamorphose is probably given by the purely physical nature of the bottom deposit, a further experiment was devised to rule out, as far as possible, the chance that the most effective bottom deposits (Bullhill sand and Penrhyn Bay sand) contained some substance that by slowly dissolving out was perceived by the larvae in a chemical manner. These two sands were therefore treated in various ways. In the acid treatment strong hydrochloric acid was followed by sulphuric bichromate solution such as is used in cleaning glassware, and finally well washed. Sand was also twice boiled, treated with absolute alcohol, and heated to redness for over 10 min. Sands thus treated were compared with the natural sands which were merely washed in fresh and sea water, without sterilization by boiling as is usual in most experiments. In these latter sands a few living nematodes were seen. Unsterilized Penrhyn Bay sand in which some adult *Ophelia* had been kept was also used to see if the adults could impart something to the sand which would make it more attractive to the larvae. A living adult *Ophelia* was also put into an otherwise clean dish. The larvae used were from the same fertilization as those of Exp. 4, but it was 3 days later that this experiment was set up and by that time many of the larvae in the culture bowls were already attached by their anal papillae to the bottom. However, some were still swimming and it was these swimming larvae which were used.

The results of this experiment are shown in Table V. It was not possible to search all the sands exhaustively though the major portion of that in each dish was examined for 20 min. or so. No significant differences are to be noted between any of the results, and it seems evident that previous treatment of the sands in the manner described had no observable effect on the reactions of the larvae towards them. At the end of the experiment the larvae and young worms were several days older than at the conclusion of Exp. 4; this and the fact that their metamorphosis had already been delayed several days before the experiment was set up probably accounts for their often poorer condition. Also in setting up this experiment larvae were removed from two separate culture bowls (both, of course, of the same age), and it may be that those in one bowl were by that time not as healthy as those in the other, with corresponding results in the dishes they were put into. At any rate, there is no obvious correlation of the state of health with the kind of sand used or with its previous treatment. To the extent that the larvae were relatively old when the experiment started and that two separate culture bowls instead of one were used the experiment is unsatisfactory, but the main purpose for which it was devised seems to have been attained. It again shows that the physical size

TABLE V. EXPERIMENT 5

(Begun 9. vii. 46 with larvae from a fertilization of 1. vii. 46.)

	15. vii. 46 and 16. vii. 46			
Clean dish	(**a**) Unmet. 11	(**b**) *c.* 12	(**c**) Metd 7 Meting 5 Unmet. 61, *d* 7	Fairly healthy. Metd worms lethargic
Bullhill sand washed in fresh water and sea water	(**a**) None	(**b**) None	(**c**) Metd 31 Meting 0 Unmet. 0, *d* 1	Healthy
Penrhyn Bay sand washed in fresh water and sea water	(**a**) Unmet. 3	(**b**) None	(**c**) Metd 31 Meting 1 Unmet. 0, *d* 2	Fairly healthy
Bullhill sand acid treated	(**a**) None	(**b**) None	(**c**) Metd 33 Meting 5 Unmet. 6, *d* 3	Healthy
Bullhill sand twice boiled	(**a**) None	(**b**) None	(**c**) Metd 23 Meting 6 Unmet. 2, *d* 6	Unhealthy
Bullhill sand heated to redness	(**a**) None	(**b**) None	(**c**) Metd 36 Meting 3 Unmet. 9, *d* 12	Majority of metd healthy, all the unmet. unhealthy
Bullhill sand washed in absolute alcohol	(**a**) None	(**b**) None	(**c**) Metd 24, *d* 1 Meting 3 Unmet. 2, *d* 4	Health poor
Penrhyn Bay sand acid treated	(**a**) ? Meting 2	(**b**) None	(**c**) Metd 25 Meting 5 Unmet. 1, *d* 6	Moderately healthy
Penrhyn Bay sand after contact with *Ophelia*	(**a**) None	(**b**) None	(**c**) Metd 21, *d* 1 Meting 1, *d* 1 Unmet. 0, *d* 3	Fairly healthy
Clean dish with adult *Ophelia*	—	—	All unmet.; mainly dead	—

(**a**) on surface film; (**b**) swimming freely; (**c**) in sand or on the bottom.

and shape of the deposit particles rather than the presence of any dissolving chemical substance is most probably the factor inducing metamorphosis, although chemical stimulus is not entirely ruled out by it.

DESCRIPTIONS OF THE SANDS USED

By the conclusion of Exp. 5 the breeding season for 1946 was virtually over and no more really healthy fertilizations were obtained that year. In the following year good fertilizations were not obtained until early in June, the breeding season having been delayed perhaps by the unusually severe weather of the previous winter; it was very cold from about the middle of January to the end of February 1947. The new series of experiments was planned to obtain more precise information about the physical characters of sand in which larvae would readily metamorphose and to determine, if possible, whether anything in the nature of a soluble substance played any part. With this end in view various sands were chosen and graded well in advance of the breeding season. The grading was done by drying the sands and passing them through simple sieves made from selected grades of new bolting silk tightly held between close-fitting metal sleeves. The silks selected were those in stock in the laboratory and had 26, 40, 60, 86, 100 and 200 meshes to the inch. Each sample of sand was washed in fresh water and thoroughly dried; it was then passed in succession through the various silks from the coarsest to the finest, so that eventually its component particles were separated out into a series of grades of nearly uniform particle size. The separated grades were kept in clean screw-stoppered jars ready for use. Each grade is designated according to the silks used to separate it. Thus grade 40–60 mesh means sand which has passed forty meshes to the inch but has been retained by sixty.

The sands treated in this way were as follows. In order to have an independent opinion as to their composition I asked Dr A. G. Lowndes to examine and describe a specimen of each, which he very kindly consented to do.

(1) *Bullhill Bank sand* from an area where adult *Ophelia* were collected in quantity. It is a very clean sand (Pl. XVI, fig. 1), 'homogeneous in size; large grains rounded; mineral chiefly quartz, tourmaline in small quantities; small amount of shell; ferruginous material. The 40–60-mesh grains are distinctly rounded, few fragmented, but in the 86–100-mesh sizes (Pl. XVI, fig. 2) more angular fragments are present, although the majority of the grains are still rounded (A.G.L.).'

The proportions by weight (per 100 g.) of the various grades were:

Mesh	g.
Larger than 26	0·25
26– 40	4·17
40– 60	59·37
60– 86	32·81
86–100	3·12
100–200	0·27
Total	99·99

(2) *Exmouth high-water sand.* This was collected from just below the promenade at Exmouth. It was well above ordinary high-water mark and certainly contained no living *Ophelia.* It was very clean and of the same or very similar mineral content, but contained a higher proportion of small pebbles: 'quite large rounded pebbles, some of which contain crystals of tourmaline; quartzite pebbles and rounded crystals of quartz; many small angular quartz fragments; fragments of shell; calcite; many pebbles of local rock (shale) up to 5 mm. The 40–60-mesh grains are distinctly rounded but in the 86–100-mesh sizes the majority are angular, though a fair proportion are rounded (A.G.L.).'

The proportions by weight were:

Mesh	g.
Larger than 26	46·00
26– 40	9·00
40– 60	22·80
60– 86	13·00
86–100	8·00
100–200	0·64
Total	99·44

(3) *Salthouse Lake sand.* This sand was collected during a brief excursion across the channel separating the Salthouse Lake area from the Bullhill Bank. It was about a quarter of a mile from the main collecting ground for *Ophelia,* but at a slightly lower tidal level. In character the shore where it was taken was quite different from the Bullhill Bank, the sand being firmer and finer with a little admixture of mud. *Arenicola marina* was abundant, with *Tellina tenuis* and a general and quite rich sand fauna. Casual digging did not turn up any *Ophelia,* though in a nearby region this species was present, in much smaller numbers than on the Bullhill Bank (personal communication from Mr N. A. Holme).

An analysis of this small sample (about 25 g.) gave the following composition:

Mesh	g.
Larger than 26	Nothing
26– 40	0·12
40– 60	1·40
60– 86	21·60
86–100	53·40
100–200	22·08
Total	98·60

It will be seen from the figures that this sand was much finer than that of the Bullhill Bank. When thrown into water a slight cloudiness was left behind after the sand had settled, showing the presence of very fine particles. A few grains passed the 200 mesh, but the amount was very small indeed. This sand (Pl. XVI, fig. 3) was 'homogeneous, medium grained, consisting of grains of quartz chiefly, angular not rounded; grains of tourmaline fairly abundant; small fragments of shell (A.G.L.)'. The mineral composition appeared to be very similar to the Bullhill Bank and Exmouth high-water sands.

(4) *Kames Bay sand.* This was sand from Millport, Isle of Cumbrae. It is finer (Pl. XVI, fig. 4) than that of the Bullhill Bank and not quite so clean. 'A clear homogeneous sand impregnated with iron; grains angular with very little rounding; small amount of shell fragments and echinoid spines; no tourmaline; a little zircon (A.G.L.).' The mineral content was not quite the same. The noteworthy feature of this sand is that it was inhabited by an allied species of *Ophelia*, the much smaller *O. cluthensis* McGuire, and the sand used came from a place where these worms were very numerous. The proportions of the various grades by weight were:

Mesh	g.
Larger than 26	0·32
26– 40	1·93
40– 60	24·51
60– 86	52·90
86–100	19·35
100–200	0·96
Total	99·97

(5) *Penrhyn Bay sand.* As already mentioned, this came from a shore in north Wales where *Ophelia*, although not extensively looked for, is almost certainly absent. It is a sand (Pl. XVII, fig. 1), 'homogeneous in size, fairly coarse; quartz and shell fragments; grains angular and rounded in about equal proportion. No tourmaline (A.G.L.)'. There are more shell fragments in this sand than in that from the Bullhill Bank. The proportions by weight of its various grades showed that it was a finer sand than that of the Bullhill Bank. These proportions were:

Mesh	g.
Larger than 26	0·23
26– 40	2·12
40– 60	36·32
60– 86	48·58
86–100	10·37
100–200	2·35
Total	99·97

(6) *Polzeath sand.* A sand (Pl. XVII, fig. 2) consisting of a very high proportion of broken shell fragments. 'At least 50% shell fragments, all polished with rounded corners; angular quartz fragments; grains of local shale and grits; very few small grains (A.G.L.).' The finer mesh sizes contained a higher proportion of angular fragments than the natural sand or the coarser mesh sizes. The proportions of the various grades by weight were:

Mesh	g.
Larger than 26	0·27
26– 40	5·43
40– 60	37·22
60– 86	43·47
86–100	12·77
100–200	0·54
Total	99·70

From this it will be seen that it was rather similar in grade to sand from the Bullhill Bank. In all other features it was a sand of quite a different character.

(7) '*Gritty' sand*. This was a sand of uncertain origin; it probably came from a dredging in deep water. It was found in an unlabelled bottle in the laboratory and seemed very suitable for use as a contrast to the other sands. It consisted of sharply angular mineral particles mixed with broken and rather sharp fragments of mollusc shells, *Echinus* spines and plates, etc. 'Rather coarse but homogeneous with a large number of shell fragments, many quartz grains and mica shale; very angular (A.G.L.).' This sand is referred to as 'Gritty' sand, and has already been mentioned by that name when describing the 1946 experiments. In that year, however, the sand was sifted under water to remove the larger fragments, sufficient of the smaller particles being removed with a pipette to form the 'fine gritty sand' (Pl. XVII, fig. 3) of those experiments. The quantity so used was less than half a gram, and hence was not very suitable for grading by the rather rough method used. However, a careful estimation gave the following result, worked out to 100 g. for comparison with other sands:

Mesh	g.
Larger than 26	Nothing
26– 40	Nothing
40– 60	1·6
60– 86	5·4
86–100	27·3
100–200	65·5
Total	99·8

Nothing passed the 200-mesh silk. It will be seen that this artificially selected sand consisted mainly of very small particles.

For the 1947 experiments the 'Gritty' sand in its original state as found in the bottle was graded and several of the grades were used as such, as will be noted under the various experiments. The ungraded sand was not so used, so that an analysis of it is unnecessary.

(8) *B.D.H. sand*, purified by acid. This is a laboratory reagent. Two grades supplied by the British Drug Houses Ltd. were used, 30–40 mesh and 60–80 mesh. By mixing these and regrading through the silks, sands of coarser, finer and intermediate grades were obtained. In composition it consisted of 'large rounded grains of quartz and small angular grains; very little ferruginous material; grains containing sillimanite and natiolite (A.G.L.)'. The sand was pale cream in colour.

The Experiments of 1947

Experiment 6

This is the first of the experiments in which graded sands were used. Various grades of Bullhill Bank sand were compared with natural Bullhill Bank, graded B.D.H. acid purified, and a coarse and fine grade of 'Gritty' sand. A clean dish served as a control.

TABLE VI. EXPERIMENT 6

(Begun 13. vi. 47 with larvae from a fertilization of 9. vi. 47.)

	23. vi. 47 and 24. vi. 47				27. vi. 47	
Clean dish	(a) Unmet. 40	(b) A few	(c) Unmet. a large number	Healthy	None metd though some prototrochal cilia lost. One may be meting	Moderately healthy
Bullhill Bank sand	(a) Unmet. 12	(b) One	(c) Metd 5 Meting 4 Unmet. but possibly meting 12	Healthy	(c) Metd 13 Meting 1 Possibly meting 2 Unmet. 3	Metd fairly healthy, others unhealthy
Bullhill Bank, 26–40 mesh	(a) Unmet. *c.* 60	(b) None	(c) Metd 6 Meting 9 Unmet. but possibly meting 8	Healthy	(c) Metd 15 Meting 1 Unmet. 3	Mainly unhealthy
Bullhill Bank, 40–60 mesh	(a) Unmet. *c.* 30	(b) None	(c) Metd 6 Meting 5 Unmet., some possibly meting 7	Healthy	(c) Metd 21 Meting 6 Unmet. 1	Some fairly healthy, others unhealthy
Bullhill Bank, 60–86 mesh	(a) Unmet. *c.* 35	(b) None	(c) Metd 7 Meting 6 Unmet., some possibly meting 9	Healthy	(c) Metd 14 Meting 6 Unmet. 3	Some fairly healthy, others unhealthy
Bullhill Bank, 86–100 mesh	(a) Unmet. 70–80	(b) Two	(c) Metd 6 Meting 10 Unmet. 42	Healthy	(c) Metd 3 Meting 6 Possibly meting 5 Unmet. 14	Mainly unhealthy

B.D.H. sand, acid purified, 26–40 mesh	(a) Unmet. 10	(b) None	(c) Metd 4 Meting 8 Unmet. 8	Unhealthy	Not examined	—
B.D.H. sand, acid purified, 40–60 mesh	(a) Unmet. 15	(b) None	(c) Metd 2 Meting 9 Unmet. 7	Unhealthy	Not examined	—
B.D.H. sand, acid purified, 60–86 mesh	(a) Unmet. 14	(b) None	(c) Metd 0 Meting 4 Unmet. 9	Unhealthy	Not examined	—
B.D.H. sand, acid purified, 86–100 mesh	(a) Unmet. 8 Possibly meting 1	(b) None	(c) Metd 0 Meting 2 Unmet. 16 Abnormal unmet. 2	Unhealthy	Not examined	—
‘Gritty’ sand, 40–60 mesh	(a) Unmet. 16	(b) None	(c) Metd 0 Meting 2 Possibly meting 10 Unmet. 15	Fairly healthy	(c) Metd 6 Meting 4 Possibly meting 2 Unmet. 3	Unhealthy
‘Gritty’ sand, 86–100 mesh	(a) Unmet. 16	(b) None	(c) Metd 2 Meting 2 Possibly meting 2 Unmet. 17, *d* 1	Fairly healthy	(c) Metd 1 Meting 1 Possibly meting 4 Unmet. 5	Fairly healthy

(**a**) on surface film; (**b**) swimming freely; (**c**) in portion of sand or on bottom.

The same volume of sand (a level saltspoonful) was used in each instance, and each quantity was separately boiled, well rinsed in tap water and then given several washings in filtered sea water from outside the breakwater ('outside water'). All dishes were acid-cleaned and well washed. Larvae used were from a batch of eggs naturally shed and fertilized on 9 June 1947. These eggs had been transferred from circulation water to outside water and gave rise to a strong healthy culture of larvae. A small quantity of autotrophic flagellates from laboratory cultures was added to supply food if needed.

To make sure of providing the larvae with opportunities to metamorphose as soon as they were ready to do so, the experiment was set up early at a time when they were not showing any tendency to attach themselves by the anal papillae and the third setiger had not developed bristles. This was probably a mistake, for as it turned out many of the larvae got caught on the surface film, or stuck themselves thereto, before they were ready to metamorphose. Moreover, by starting the experiment early the dishes had to stand without change of water for a longer period than would otherwise have been necessary, and this may have been partly responsible for the poor health of the larvae at the end of the experiment.

In Table VI the results are set out. The larvae on the surface films were removed from the influence of the sands and must therefore be ignored in considering the results. Metamorphosis was seen to have begun in some of the sand pots on 21 June, that is, 8 days after the larvae had first been put in the dishes. A careful examination of each pot was started on 23 June and finished the next day. In every instance all larvae on the surface film were carefully removed with a pipette before a little of the sand was taken out and searched. Searching took about 15 min. or longer; in the 'Gritty' sands the larvae were particularly hard to see, and with each of these the time of searching was extended to about an hour. The 86–100 grade of Bullhill Bank sand was searched for half an hour. In the semi-transparent colourless grains of the B.D.H. sand the larvae were clearly visible, and easily found. The sands which had been removed and searched and the larvae found in them were not returned to the dishes but were discarded, as were all the larvae on the surface films.

It is obvious that only the numerical proportions between unmetamorphosed, metamorphosing and metamorphosed larvae are significant, and this must be borne in mind when comparing dish with dish. In numerous instances it was very difficult to distinguish between larvae which were unmetamorphosed and those which had perhaps begun to metamorphose. Where necessary this is indicated in the table. It will be seen that all the Bullhill Bank sands except the 86–100 grade show very similar results, but the latter seems quite definitely to have a small proportion of its larvae metamorphosed or metamorphosing. Some of the larvae were stuck together in clusters of several individuals, but all were healthy, as, indeed, were all those in Bullhill sand. On the other hand, all the larvae in the B.D.H. pots were markedly unhealthy, though here again the finest grade used had a higher proportion of unmetamorphosed larvae than did the others. In both coarse and fine 'Gritty' sands only a small proportion had metamorphosed or were metamorphosing; the health of these dishes was fairly good.

On 27 June a final examination was made. In the clean dish the larvae were still unmetamorphosed with some not very active cilia on their prototrochs, and they were moderately healthy. In all the Bullhill sands except the finest grade metamorphosed larvae greatly preponderated over unmetamorphosed, while the reverse was true for the 86–100 grade. The results for the 'Gritty' sands were not good, but they do show something similar when coarse and fine grades are compared, though here the coarser grade does not appear to be as effective in producing metamorphosis as the corresponding grade of Bullhill sand. The B.D.H. sands were unhealthy on the first examination on 24 June and therefore were not re-examined on 27 June.

Experiment 7

This experiment was similar in conception to the last, only here various mesh sizes of Exmouth high-water sand were tested. This sand was the nearest sort to the Bullhill sand in which it was certain that adult *Ophelia* had not been living. In addition, other sands of quite different types were also tested. The same preliminary sterilizations and washings of the sand were carried out as for Exp. 6 and larvae from the same fertilization were used. The experiment was set up 2 days later than Exp. 6, but even so an unduly large proportion of the larvae attached themselves to, and thereby became trapped on, the surface film. The dishes were first looked at 10 days after the experiment began, and the examination of the various dishes took 2 days to complete. The results are shown in Table VII. All the larvae and sands removed from the dishes on 25 and 26 June for counting were discarded and not returned to the experiment. Great care was taken to remove all larvae on the surface film before disturbing the sand. A little filtered sea water was added to several of the dishes to make up for that lost by removal of these larvae. Some of the dishes were examined again on 4 July.

Once again the larvae metamorphosed more readily in the Bullhill sand than in any of the other sorts and, moreover, were, on the whole, considerably healthier than in the other dishes. The various grades of the Exmouth high-water sand gave unexpectedly poor results; it was thought that the 40–60- and 60–86-mesh sizes would have induced a high proportion of larvae to metamorphose. Grains of these sizes form the bulk of the Bullhill sand, and there is little difference in geological character between the latter and the sand from high-water mark a mile or so away. The high-water grains tend to be a little more angular, but except for the smallest sizes this is not very noticeable. The larvae in the dish containing 40–60-mesh size high-water sand were not really

TABLE VII. EXPERIMENT 7

(Begun 15. vi. 47 with larvae from a fertilization of 9. vi. 47.)

	25. vi. 47			26. vi. 47			4. vii. 47	
Clean dish I	(a) Unmet. 33	(c) Unmet. *c.* 70	Healthy	—	—	—	(c) Majority umet, but 3 or 4 metd and a few possibly meting	Health poor
Clean dish II	—	—	—	(a) Possibly meting 1 Unmet. *c.* 35	(c) Possibly meting 1 or 2 Unmet. 70–80	Very healthy	All unmet.	Moderately healthy
Bullhill Bank sand	(a) Unmet. *c.* 70	(c) Metd 14 Meting 5 Unmet. 2	Very healthy	—	—	—	(c) Metd 15 Meting 2 Unmet. 0	Fairly healthy
Exmouth high water retained by 26 mesh	(a) Unmet. *c.* 60	(c) Metd 3 Meting 10 Unmet. 41	Healthy	—	—	—	—	—
Exmouth high water, 26–40 mesh	(a) Unmet. *c.* 100	(c) Metd 1 Meting 0 Unmet. 15	Healthy	—	(c) Metd 0 Meting 1 Unmet. 17	Moderately healthy	—	—
Exmouth high water, 40–60 mesh	(a) Unmet. 70	(c) 1st count 2nd count Metd 5 6 Meting 12 10 Unmet. 5 1	Moderately healthy	—	(c) Metd 5 Meting 4 Probably meting 2 Early meting 9	Unhealthy	—	—
Exmouth high water, 60–86 mesh	(a) Unmet. *c.* 60	(c) Metd 1 Meting 3 Unmet. 16	Healthy	—	(c) Metd 0 Meting 1 Unmet. 5	Moderately healthy	—	—
Exmouth high water, 86–100 mesh	(a) Unmet. *c.* 50	(c) Metd 2 Meting 7 Unmet. 22	Quite healthy	—	—	—	—	—
Exmouth high water, 100–200 mesh	(a) Unmet. *c.* 70 Meting 1	(c) Metd 0 Meting 6 Unmet. 40	Fairly healthy	—	—	—	—	—
Salthouse Lake sand	—	—	—	(a) Unmet. *c.* 30	(c) Metd 0 Meting 2 Possibly meting 4 Unmet. 18, *d* 1	Health poor	(c) Metd 5 Meting 2 Unmet. 0	Health poor
Kames Bay sand	—	—	—	(a) Unmet. *c.* 30	(c) Metd 3 Meting 6 Possibly meting 7 Unmet. 20	Moderately healthy	(c) Metd 17 Meting 1 Unmet. 0	Fairly healthy
Kames Bay recombined in proportions of Bullhill sand	(a) Unmet. *c.* 80	(c) Metd 0 Meting 2 Possibly meting 4 Unmet. 11	Moderately healthy	—	—	—	—	—
Polzeath, 40–60 mesh	—	—	—	(a) Unmet. *c.* 25	(c) Metd 0 Meting 0 Possibly meting 1 Unmet. 20	Very healthy	(c) Metd 5 Meting 1 Unmet. 0	Fairly healthy
Polzeath, 60–86 mesh	—	—	—	(a) Unmet. 50–60	(c) Metd 0 Meting 1 Possibly meting 2 Unmet. 23	Moderately healthy	(c) Metd 10 Meting 10 Unmet. 0	Moderately healthy
Polzeath recombined in proportions of Bullhill sand	—	—	—	(a) Unmet. *c.* 80 1 or 2 may be meting	(c) Metd 0 Meting 1 Possibly meting 3 Unmet. 24	Healthy	—	—
‘Gritty’ sand recombined in proportions of Bullhill sand	—	—	—	(a) Unmet. *c.* 15	(c) Metd 2 Meting 4 Possibly meting 5 Unmet. 15	Moderately healthy	—	—

healthy, and it may be that some infection in this dish affected the result. The larvae in the 60–86-mesh dish were fairly healthy, however, and yet showed an even more marked reluctance to metamorphose. In the other sands metamorphosis was delayed compared with the Bullhill sand, although in most of them larvae did eventually succeed in metamorphosing. The vast majority of the larvae in the two clean dishes were still unmetamorphosed at the end of the experiment.

A few words should be inserted here on the condition of the unmetamorphosed larvae. On 25 and 26 June those on the surface film of all dishes had strong prototrochal cilia and almost certainly apical tufts and telotrochs as well. With the dissecting binocular used in this work it was not very easy to see cilia other than those forming the prototroch which when present was always clearly visible. On the same dates the unmetamorphosed larvae in the various sands also nearly always had good prototrochs and could generally swim well when disturbed, but in a number the ciliation was rather irregular and a few had lost most of the cilia, though otherwise retaining the prototrochal tissue. By 4 July few of the unmetamorphosed larvae, even those on the surface film, retained any of their cilia, although the other tissues of the prototroch were clearly visible. The general health conditions were, however, poor, and this may have been partly responsible for this loss of tissue. On this date it was, indeed, difficult to classify the larvae properly at all, and some of those put down as metamorphosing may possibly have been fully metamorphosed but imperfectly formed.

Some of the unmetamorphosed larvae on the surface films were stuck together by their anal papillae in little clusters and some surrounded cotton fragments, though a great many were attached to the film singly. In the sands, particularly the two finest grades from Exmouth high water, there were also little clusters of larvae; these were sometimes visible on the surface of the sand before the latter was disturbed.

Experiment 8

The tests of the Exmouth high-water sand made in the last experiment not having proved very satisfactory on account of the unhealthy state of several of the dishes, it was decided to try the various grades again and at the same time to include a graded series of Bullhill sand. In addition to these, the four grades 26–40, 40–60, 60–86 and 86–100 mesh of both Bullhill and Exmouth high-water sands were recombined in the correct proportions by weight to resemble Bullhill Bank sand. These recombined sands lacked only particles larger than 26 mesh and smaller than 100 mesh, both of which, as shown on p. 734, are present in the natural Bullhill sand in very small proportion only. To one of the recombined Exmouth high-water sands a little Bullhill Bank natural sand was added. Some further tests with Carborundum grit No. 120 (Pl. XVII, fig. 4) were also included, but in the mixture with Bullhill natural sand only about a third part was Carborundum—a smaller proportion than in

Exp. 4. The grit did not mix uniformly with the sand, and there were patches of the latter almost free from it.

On the whole this experiment was much healthier than the preceding two and there was never any difficulty in deciding to which category a larva belonged, as was rather often so in Exps. 6 and 7. The unmetamorphosed were strongly ciliated, short in body and without long bristles, the metamorphosing were distinctly elongating with narrow and interrupted prototrochs which still retained some cilia, and the bristles were elongating. The metamorphosed had no less distinctly lost all cilia, were elongated and had long bristles, especially on the third setiger. Individuals rarely departed from these standards[1] which were not always so closely followed in other experiments. This variation in health of different experiments was probably to a large extent due to variation in the state of maturity of the eggs and sperms at fertilization.

The main results of Exp. 8 are set out in Table VIII. The experiment was started on 9 July with 6-days-old larvae which were swimming strongly, though occasionally using the anal papillae to attach themselves to the sides of the glass bowl in which they were kept. Attachment was always only temporary; attached larvae easily released themselves and swam away again. They were strongly negatively phototropic; there were no bristles on the third setiger. The sands and dishes were cleaned and sterilized as described for Exp. 6; a new feature was a black paper collar around each dish so that light came only from above, and the dishes were stood on black paper. It was hoped by this means to drive the negatively phototropic larvae away from the surface film. Unfortunately, many larvae were again trapped, perhaps at night but also certainly by day as well. On 11 July larvae on the surface film were released by dropping freshly filtered outside sea water on to them from a pipette, but they were soon back again. On that day several fully metamorphosed larvae were observed in the sands of some of the dishes. It was intended to make a count on 13 and 14 July, but this could not be done until 15 and 16 July.

All larvae on the surface films were carefully removed before the sands were disturbed. There were always large numbers of these except in one or two instances where the dish was so full of water that the watch-glass dust-cover dipped below the surface and so reduced the area of water-air interface. In future experiments it may be possible to devise some such means of avoiding this particular trouble with the larvae. Before the dishes were disturbed care was always taken to note whether any larvae were swimming freely and whether any could be seen on the surface of the sand. It was impossible within the time available to search all the sands; a portion only was removed from each dish for this purpose.

It had been noted in the previous experiment that larvae often tended to stick together in clusters, especially unmetamorphosed larvae on unsuitable sands. In this experiment therefore clusters are recorded as such, the number of larvae forming each cluster being noted. Such clusters could often be observed lying on the surface of the sand before any of the latter was removed for examination.

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[1] The general appearance of these stages is shown in Plate XV, figs. 1–3, which are of larvae from an experiment in 1948.

Some of the results of this experiment are clear and definite. Larvae in the clean dish and those on the surface films of all the other dishes were still unmetamorphosed some time after many in contact with sand had undergone the critical change. The ungraded, or natural sand from the Bullhill Bank was rarely equalled by any of the graded sands in its property of stimulating larvae to metamorphose. Of the graded sands the 40–60 mesh from Exmouth high water gave a result comparable with that of the Bullhill Bank natural, and there was a marked reduction in efficiency of coarser and finer grades. In the graded Bullhill Bank sand of the 40–60-mesh size the larvae did not seem to be quite as healthy as was usual in this experiment, and this probably affected the result. None the less this grade did on the whole yield a higher proportion of metamorphosed worms than the others, though less than could reasonably be expected. In the two finest grades of both sorts of sand only a very few larvae metamorphosed; in these dishes the great majority of the larvae were unchanged and were often stuck together in clusters of several individuals. The sands recombined from four sifted grades were variable in their effect, though some of the Exmouth recombined sands were almost as efficient as the Bullhill Bank natural. Carborundum grit again had a marked effect, changing the properties of the Bullhill Bank natural sand to which it was added, and in itself proved an unsuitable medium for larval settlement.

It will be noted that there is a difference in result between the two dishes of Bullhill Bank natural sand. In the first dish twenty healthy metamorphosed worms were counted in 5 min. and many more seen, whereas in the second dish 10 min. searching yielded only nineteen metamorphosed and about half as many unmetamorphosed larvae. It is possible that fewer larvae had originally been put into this dish than into the first one. It was noticed that the larvae and worms in the second dish were not as healthy as in the first dish, and this may have been a prime cause in influencing the result. These differences in health between dish and dish may be due to chance bacterial infection; it is impracticable to conduct experiments of this nature under bacteriologically sterile conditions. The small number of larvae on the surface film of the second dish was due to the bottom of the watch-glass cover dipping into the water so as almost to obliterate the air-water interface normally present.

The experiment was completed on 16 July, but the clean dish was kept and examined again on 23 July, the larvae by then being 20 days old. Some of the larvae had metamorphosed, both on the surface film and on the bottom, but were imperfectly formed, and some were metamorphosing. Other larvae were still unmetamorphosed, but had lost most or all of the prototrochal cilia.

TABLE VIII. EXPERIMENT 8

(Begun 9. vii. 47 with larvae from a fertilization of 3. vii. 47.)

	15. vii. 47			
Clean dish	(a) All unmet.	—	(c) All unmet.	Very healthy
Bullhill Bank sand, dish No. 1	(a) Unmet. *c.* 150	(b) None	(c) Single: Metd 20+ Meting 0 Unmet. 0 Clusters: *None*	Very healthy
Bullhill Bank sand, dish No. 2	(a) Unmet., a few	(b) None	(c) Single: Metd 19 Meting 4 Unmet. 9, *d* 2 Clusters: Unmet. *2*	Fairly healthy
Bullhill Bank, 26–40 mesh	(a) Unmet., large number	(b) None	(c) Single: Metd 10 Meting 8 Unmet. 9 Clusters: Unmet. *4, 5, 6*	Healthy
Bullhill Bank, 40–60 mesh	(a) Unmet., many	(b) None	(c) Single: Metd 12 Meting 4 Unmet. 6 Clusters: Unmet. *4, 5, 5*	Some unhealthy, others moderately healthy
Bullhill Bank, 60–86 mesh	(a) Unmet., large number	(b) Several	(c) Single: Metd 11 Meting 7 Unmet. 9 Clusters: Meting *2* Unmet. *4, 8, 3, 4, 7*	Moderately healthy
Bullhill Bank, 86–100 mesh	(a) Unmet., large number	(b) A few	(c) Single: Metd 5 Meting 4 Unmet. 7 Clusters: Meting *2* Unmet. *4, 5, 6, 4, 8, 7*	Very healthy
Bullhill Bank, 100–200 mesh	(a) Unmet. 150–200	(b) None	(c) Single: Metd 0 Meting 0 Unmet. 8 Clusters: Unmet. *4*	Healthy
Bullhill Bank, four grades recombined, dish No. 1	(a) Unmet., large number	(b) Several	(c) Single: Metd 12 Meting 6 Unmet. 10 Clusters: Meting *3* Unmet. *2*	Healthy
Bullhill Bank, four grades recombined, dish No. 2	(a) Unmet., large number	(b) Several	(c) Single: Metd 7 Meting 3 Unmet. 5 Clusters: Unmet. *3, 2, 2*	Moderately healthy
Bullhill Bank and Carborundum	—	—	—	—
Carborundum grit No. 120	—	—	—	—
Exmouth high water, 26–40 mesh	(a) Unmet., large number	(b) Several	(c) Single: Metd 14 Meting 2 Unmet. 8 Clusters: Unmet. *5, 2, 3, 2*	Healthy
Exmouth high water, 40–60 mesh	(a) Unmet., many	(b) None	(c) Single: Metd 28 Meting 2 Unmet. 2 Clusters: None	Healthy
Exmouth high water, 60–86 mesh	(a) Unmet., large number	(b) 1 or 2	(c) Single: Metd 12 Meting 7 Unmet. 11 Clusters: Meting *3* Unmet. *8, 3, 2*	Healthy
Exmouth high water, 86–100 mesh	(a) Unmet., large number	(b) None	(c) Single: Metd 7 Meting 1 Unmet. 7 Clusters: Unmet. *4, 4, 3, 14, 6, 6, 6, 4, 4, 6, 7*	Healthy
Exmouth high water, 100–200 mesh	(a) Unmet., large number	(b) None	(c) Single: Metd 2 Meting 1 Unmet. 9 Clusters: Unmet. *9, 2, 5, 10, 6, 5, 6, 7, 2, 12, 3, 10, 8, 5, 3, 7, 5*	Healthy
Exmouth high water, recombined as Bullhill Bank, dish No. 1	(a) Unmet. 175–200	(b) None	(c) Single: Metd 16 Meting 4 Unmet. 7 Clusters: Unmet. *5, 5, 7, 5*	Very healthy
Exmouth high water, recombined as Bullhill Bank, dish No. 2	(a) Unmet. *c.* 150	(b) None	(c) Single: Metd 30 Meting 5 Unmet. 1, *d* 2 Clusters: Meting *5* Unmet. *6*	Very healthy
Exmouth high water, recombined as Bullhill Bank, dish No. 3	(a) Unmet., large number	(b) None	(c) Single: Metd 22 Meting 1 Unmet. 0 Clusters: Metd 2 Unmet. *5, 6*	Healthy
Exmouth high water, recombined + a little Bullhill sand	—	—	—	—

TABLE VIII. EXPERIMENT 8 (*cont.*)

16. vii. 47			
One on bottom meting. Bristles of third setiger very short	Others all unmet. with strong prototrochs and apical tufts.		Healthy
—	—	—	—
(a) Unmet. 70–80	(b) None	(c) Single: Metd 39 Meting 2 Unmet. 5, *d* 11 Clusters: Meting *4* Unmet. *9, 5, 2, 2, 4*	Metd moderately healthy; unmet. unhealthy
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
(a) Unmet., large number	(b) A few	(c) Single: Metd 29 Meting 14 Unmet. 10 Clusters: Unmet. *4, 3*	Fairly healthy
(a) Unmet., fairly large number	(b) A few	(c) Single: Metd 15 Meting 5 Unmet. 15 Clusters: Unmet. *6, 3, 2*	Fairly healthy
(a) Unmet., many	(b) None	(c) Single: Metd 6 Meting 4 Unmet. 23 Clusters: Unmet. *6, 4*	Poor health
(a) Unmet., a few	(b) None	(c) Single: Metd 0 Meting 0 Unmet. 23, *d* 22 Clusters: Unmet. *2, 2, 2, 3, 5, 10, 2, 4, 4* Unmet. *d 3, 2, 2, 2, 2, 2*	Some healthy, but others unhealthy
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
(a) Unmet., a few	(b) None	(c) Single: Metd 0 Meting 0 Unmet. 1 Clusters: Unmet. *3, 5, 7, 10, 6*	Healthy
—	—	—	—
—	—	—	—
(a) Unmet. *c.* 50	(b) 1 or 2	(c) Single: Metd 34 Meting 3 Unmet. 1 Clusters: Meting *5*	Healthy
(a) Unmet., many	(b) None	(c) Single: Metd 38 Meting 4 Unmet. 1 Clusters: Unmet. *2*	Healthy

(a) on surface film; (b) swimming; (c) on bottom or in portion of sand. The italicized figures under 'clusters' give the number of larvae per cluster, each figure representing a single cluster.

Experiment 9

This was a small experiment to test whether freshly collected and unboiled Bullhill sand was more active than sand which had been left a long time and had been boiled. The fresh sand had living *Ophelia* worms in it until used; it was washed only in warm and cold fresh water and filtered sea water. The result (Table IX) reveals no significant difference. In the same experiment two grades of 'Gritty' sand were also tested, and it is to be noted that both had almost no effect in promoting metamorphosis, although one of the grades had a grain size equivalent to that most commonly found in the Bullhill Bank. In all these dishes, and in the clean dish in which no metamorphosis took place, the larvae were strong and healthy, but in a dish containing B.D.H. acid-purified sand recombined in the proportions by weight of the Bullhill Bank sand almost all the larvae were dead or dying and none was in good condition. In all previous experiments with this sand the larvae had been adversely affected in spite of the sand being well boiled and well washed before use. The reason for this apparently lethal action (it seems too improbable to assume chance bacterial infection is the cause here) is unknown.

EXPERIMENTS ON CHOICE OF BOTTOM

In none of the experiments so far described were the larvae given a choice of sands in which to settle. Each dish contained only one kind of soil, or none at all. In order, therefore, to test the selective powers of the larvae another type of experiment was needed, one in which the larvae were afforded the opportunity to settle in one or more different kinds of sand in the same dish.

Experiment 10

This was designed to test the ability of larvae to find a small area of suitable sand placed in the centre of a large dish. A Petri dish of 9 cm. internal diameter had a small patch of Bullhill sand less than 2 cm. in diameter in the middle of the dish. A large number of actively swimming larvae were put into the dish, which was covered and left undisturbed in a cool place. This experiment began on 12 June 1946 with larvae from a fertilization of 5 June. The larvae were beginning to use their anal papillae for attachment. On 19 June the dish was carefully examined and the result is shown in Table X. There were twenty unmetamorphosed larvae stuck to the surface film, while on the bottom, away from the sand, 226 larvae were counted. Of these four were metamorphosed, but were near the sand and had probably crawled out of it. One other was metamorphosing. All the remainder were unmetamorphosed, some attached singly to the glass, but over half of them stuck to bits of cotton and other debris. One long cotton fragment had about seventy larvae attached. In the sand were seventy-nine metamorphosed healthy-looking worms with others metamorphosing and unmetamorphosed, making in all a total of 140.

TABLE IX. EXPERIMENT 9

(Begun 17. vii. 47 with larvae from a fertilization of 7. vii. 47.)

		21. vii. 47		
Clean dish	(a) Unmet. many	(b) A few	(c) Unmet. many	Healthy
12 months old Bullhill Bank natural	(a) Unmet. *c.* 100	(b) None	(c) Single: Metd 11 Meting 6 Unmet. 14 Clusters: *None*	Healthy
Freshly collected Bullhill Bank natural	(a) Unmet. *c.* 100	(b) None	(c) Single: Metd 11 Meting 7 Unmet. 8 Clusters: *None*	Healthy
'Gritty' sand, 40–60 mesh	(a) Unmet. *c.* 8	(b) Small number	(c) Single: Metd 0 Meting 3 Unmet. 13 Clusters: *None*	Healthy
'Gritty' sand, 100–200 mesh	(a) Unmet. *c.* 60	(b) A few	(c) Single: Metd 0 Meting 2 Unmet. 15 Clusters: Unmet. *2, 6, 3, 10, 12*	Healthy
B.D.H. sand, acid-purified, recombined as Bullhill Bank	(a) Unmet. *c.* 20, several dead or dying	(b) None	(c) Single: Metd 0 Meting 1 Unmet. but dead 5 Clusters: *None*	Nearly all dead or dying

(**a**) on surface film; (**b**) swimming freely; (**c**) in portion of sand. The italicized figures under 'clusters' give the number of larvae per cluster, each figure representing a single cluster.

To these should probably be added the four metamorphosed worms found on the glass close by. A simple calculation shows that in the sand larvae had congregated to the extent of about forty-eight to the sq.cm., whereas on the glass bottom the density was only about 2·4 to the sq.cm. This latter figure, of course, assumes even distribution and ignores the actual great local concentration on cotton fragments, which is probably something that would not occur in the sea.

TABLE X. EXPERIMENT 10

(Result on 19. vi. 46.)

	On surface film	On glass	In sand
Metd	0	4	79
Meting	0	1	25
Unmet.	20	83; *70, 4, 9, 6, 8, 8, 5, 8, 7, 8, 5*	36
Total	20	226	140

When clusters were present, the figures are given separately in italic, each figure representing a single cluster.

From the result it appears that larvae, once they have come into contact with the sand, tend to stay there and metamorphose. As all the larvae in the dish were not in the sand, most of them, indeed, being away from it, it seems unlikely that the sand exerts any sort of chemical attraction for them over a distance. They probably find it by chance contact while swimming about. It is probable, too, that more larvae would have reached the sand had they not first become stuck to the glass or surface film, or trapped by cotton fragments in such a manner that they were unable to detach themselves. In moving water, such as would occur in nature, it is probable that detachment from the bottom would have been facilitated. In nature, too, cotton and other dust particles can hardly be such a menace as they are in laboratory dishes.

Experiment 11

This was similar to Exp. 10, but two patches of sand were used, one of Bullhill Bank sand and the other sand from Penrhyn Bay. Each little heap of sand was about 1·5 cm. in diameter, and their centres were 4·5 cm. apart in a Petri dish of 9·0 cm. internal diameter. The dish was kept in a cupboard in the dark for the first 36 hr. and then on a cool shelf near the sea-water circulation. The experiment began on 11 July 1946 with swimming larvae from a fertilization made on 1 July 1946. The dish was examined and the larvae counted on 16 July 1946. It was found that *Skeletonema* chains and a small naviculoid diatom covered the bottom in large numbers and the larvae both on the glass and in the sands were badly fouled with them, the diatoms sticking to their bristles. A number of larvae were dead, while the living ones were in poor condition. In setting up these early experiments the water was not filtered as it was in later experiments after the necessity for so doing had become apparent.

TABLE XI. EXPERIMENT 11

(Result on 16. vii. 46.)

	On glass	In Bullhill sand	In Penrhyn Bay sand
Metd	4	34 *d* 1	8
Meting	9	2 *d* 2	1 *d* 1
Unmet.	86 *d* 24	2 *d* 5	0 *d* 3
Total	123	46	13

In spite of the poor condition of the larvae, doubtless to a large extent brought about by this excessive concentration of diatoms, the result of the experiment (see Table XI) is interesting. There was a greater concentration of larvae in the Bullhill sand than in the Penrhyn Bay sand and a greater concentration in both sands than on the glass. The figures per sq.cm. give for the Bullhill sand 20 larvae, Penrhyn Bay sand about 5·6 and for the glass 1·3 larvae. On the glass there were a few small clusters of larvae, but most of them were scattered singly about the dish.

The original notes on this experiment make no mention of larvae caught on the surface film. It can be assumed that either none was present or the numbers were small, and not being specially noteworthy were accidentally omitted when recording the result.

Experiment 12

This was similar to the last, but was made the following summer. Some slight changes were introduced in the arrangement. Smaller Petri dishes, only 7 cm. internal diameter, were used, and the sands were confined within shallow glass rings of the kind used in making microscopic mounts of large objects. These rings were of 1 cm. internal diameter; they were placed loosely on the bottoms of the Petri dishes and were not cemented into place. As usual all glassware was acid cleaned and well washed before use.

Three dishes were used; in each one or more sands were tested against Bullhill Bank sand. The experiment began on 14 June 1947 with larvae from a fertilization of 9 June. It was a healthy culture with the larvae still mainly swimming and with few attaching. The larvae actively moved away from a source of light. The dishes were kept on black paper and were covered with glass sheets and tissue paper in a cool place.

The experiment was ended on 30 June and 1 July when the dishes were examined and the larvae in the sands counted. In counting the larvae in the sands great care was taken to ensure that every one was found and it is thought improbable that any escaped observation. The results are shown in Table XII. Larvae on the surface film and bottom were noted, but not counted. In all dishes there was a large number of larvae on the surface film as well as on the bottom; clusters of larvae were often attached to cotton fragments.

TABLE XII. EXPERIMENT 12

(Result on 30. vi. 47 and 1. vii. 47.)

	Dish A		Dish B		Dish C		
	Bullhill Bank sand	Salthouse Lake sand	Bullhill Bank sand	Polzeath sand	Bullhill Bank sand	Kames Bay sand	'Gritty' sand
Metd	23	8	43	21	80	30	30
Meting	3	6	11	11	22	13	12
Possibly meting	1	9	1	9	6	8	10
Unmet.	5; *6*	13	2	15; *3, 7*	14	3; *2*	22; *6, 3*
Dead unmet.	1	1	1	2	1	1	—
Total	39	37	58	68	123	57	83

When clusters were present, the figures are given separately in italic, each figure representing a single cluster.

From Table XII it will be seen at once that as in so many other experiments the Bullhill Bank sand yielded more fully metamorphosed young worms than did sand of other kinds. Moreover, the young worms in the Bullhill Bank sand were always the healthiest of the lot, those in the Salthouse Lake sand and the Polzeath sand in particular being in rather poor condition. The total number of worms and larvae in the Bullhill Bank sand was generally larger than in the others, though unmetamorphosed larvae in some abundance raised the total figure for the Salthouse Lake, Polzeath and 'Gritty' sands. In removing the sands for examination care had been taken to avoid falsification of the result by accidental mixing with unmetamorphosed larvae from the surface film, but this may not have been avoided altogether. Clusters are to be specially suspect as having fallen into the sands from the surface film when the dishes were disturbed.

It was often difficult in this experiment to be sure of the correct classification of unmetamorphosed and metamorphosing larvae. Some of the former had lost their cilia, but no other changes were noticeable. The health of these stages in the sands was not as good as that of most of the fully metamorphosed young worms, or as good as that of the larvae on the surface film or on the glass bottom of each dish.

Although no actual calculation was made, it was obvious to the eye that the concentration of the larvae per unit area of clear glass bottom was much less than in any of the sands.

The larvae on the surface film or on the bottom were almost all unmetamorphosed, though a very few on the bottom were metamorphosed or metamorphosing, and it is just possible they may have crawled out of the sand. It was noted in all three dishes that the larvae on the surface film nearly all had strong prototrochs and apical tufts, whereas those on the glass bottom were not quite so healthy and there was some tendency to loss of cilia, some from the prototroch but especially the apical tufts, as though contact with the hard surface of the bottom served as a slight stimulus towards metamorphosis. This has also been noticed in other experiments.

While not satisfactory in every respect, this experiment does show once again the relatively greater readiness of the larvae to enter Bullhill Bank sand than any other kind, and that once there they are likely to metamorphose without delay.

Experiment 13

Three small dishes of 3 cm. internal diameter were each divided into two sections by placing across the bottom a narrow strip of glass cut from a microscope slide. On one side of the strip the bottom was covered with Bullhill Bank sand, on the other with a natural sand of another sort. Larvae could readily pass from one sand to the other by swimming over the strip. Sands were sterilized by boiling and then were well washed in fresh and filtered sea water in the usual way; the dishes were filled with filtered sea water. Larvae 5 days old were put into the dishes on 8 July 1947. Each dish was surrounded by a collar of black paper and covered by a glass plate, but as in Exp. 8, which ran concurrently, this method failed to prevent large numbers of larvae attaching themselves to the surface film.

The dishes were not examined until 18 July when it was seen that in each instance 100–200 larvae were on the surface film, almost all of them unmetamorphosed, though a few had rather long bristles on the third setiger whilst still retaining a well-ciliated prototroch. This was unusual. These surface-film larvae were carefully removed and the surfaces of the sands then searched with a low-power binocular. Several clusters of larvae stuck together were seen, as well as single unmetamorphosed larvae sitting upright on their anal papillae attached to sand grains, their prototrochs beating actively, causing heads and bodies to wave about as though endeavouring to get free. Sometimes metamorphosed worms could also be seen. The clusters were removed, as it was considered that they were to a large extent an unnatural formation due to the great concentration of larvae in a relatively small volume of water. The larvae could hardly avoid contact with particles of debris and with one another, and they readily adhered by the mucus they secreted. Thus all clusters seen on the surface were removed, but the subsequent search of the sands showed that many had become buried and the larvae forming them often metamorphosed, though it is possible that some of the clusters were formed after metamorphosis owing to the great concentration in what was relatively a very small amount of sand. Against this is the significant fact that, whereas in dish C the majority of the larvae in the clusters found in the sand were unmetamorphosed (see Table XIII), those in dishes D and E, examined 4 and 5 days later respectively, were mainly all metamorphosed, suggesting that metamorphosis of larvae clustered together does take place when the clusters are buried in sand.

TABLE XIII. EXPERIMENT 13

Dish C (examined 18. vii. 47)

	Bullhill Bank sand		Salthouse Lake sand	
	Singles	Clusters	Singles	Clusters
Metd	37	*2*	12	*None*
Meting	20	*2, 3, 3, 2*	17	*2, 2*
Possibly meting	15	*None*	11	*2*
Unmet.	23	*2, 5, 12, 6, 8, 5, 8, 3, 7, 7, 8, 6, 4, 3, 3*	31	*3, 7, 2, 6, 2, 6, 4, 5, 4, 6, 3, 6, 4, 6, 6, 3, 4*
Dead	2	—	1	*None*
Totals	97	*99*	72	*83*
		196		155

Dish D (examined 22. vii. 47)

	Bullhill Bank sand		Polzeath sand	
	Singles	Clusters	Singles	Clusters
Metd	78	*2, 3, 4, 5, 6, 6, 5, 4, 2, 5, 4, 4, 5, 2*	36	*3, 3, 4, 3, 4*
Meting	3	*2*	3	*3, 4, 2, 2, 8*
Possibly meting	None	*None*	None	*None*
Unmet.	None	*None*	3	*12, 8, 4*
Dead	None	*None*	None	*None*
Totals	81	*59*	42	*60*
		140		102

Dish E (examined 23. vii. 47)

	Bullhill Bank sand		Kames Bay sand	
	Singles	Clusters	Singles	Clusters
Metd	130	*5, 3, 5, 2, 4, 2, 4, 3, 2*	114	*3, 9, 3, 7, 5, 6, 4, 5, 9, 3, 3, 5, 6, 5, 4, 4, 5, 3, 5, 3, 2*
Meting	3	*3*	10	*6, 4*
Possibly meting	None	*None*	None	*None*
Unmet.	None	*None*	3	*4*
Dead	None	*None*	None	*None*
Totals	133	*33*	127	*112*
		166		239

The italicized figures under 'clusters' give the number of larvae per cluster, each figure representing a single cluster.

If in interpreting the results (Table XIII) only single larvae are considered, the usual relative distribution of the larvae among the sands is seen. The Bullhill Bank sand always collects most and induces earlier metamorphosis in the majority of those collected. This is also true in dishes C and D of the clusters as well, but in dish E the usual conditions as regards numbers are reversed. There is no doubt that the formation of clusters in a high concentration of larvae is an unfortunate complication in experiments of this kind, and so is the absence of natural currents to assist the detachment of larvae endeavouring to pull themselves free from surface sand grains to which they have become too strongly fastened by their anal papillae.

The health of the larvae in dish C was not very good; there were some small ciliates in this dish and some of the larvae were being attacked. In dish D the metamorphosed worms in the Polzeath sand were definitely unhealthy, stumpy and not well formed. Those in the Bullhill sand of the same dish were on the whole healthier and livelier and better formed. The health of dish E was good and the metamorphosed worms in both kinds of sand were in good condition, but again those in the Bullhill sand seemed superior in this respect. They had on the whole larger bodies, longer bristles and a generally better appearance of well-being.

General Conclusions

Additional experiments are planned for the future, and therefore it is not thought fitting at this stage to enter into a complete discussion of the results so far obtained, nor to consider exhaustively the literature bearing on the subject. Some major points have, however, emerged, and it is right that these should be summarized. Some comparison with Jägersten's remarkable results must also be made.

Jägersten (1940) worked with larvae of *Protodrilus rubropharyngeus* Jägersten which he obtained by tow-netting. In a series of extremely interesting experiments he found that in the shell gravel in which this particular species of *Protodrilus* lives, and apparently also in other gravel of similar character, there is a metamorphosis-producing substance, inorganic in nature and extremely resistant to boiling in water, incineration, treatment with alcohol, formalin, acids, etc. It can be destroyed by prolonged soaking in fresh water and by boiling for 2 hr. in nitric acid, but not by several hours' boiling in sulphuric and hydrochloric acids or sodium hydroxide. Jägersten states that quite a small fragment from shell gravel containing the substance will cause *Protodrilus* larvae to metamorphose when it is placed with them in an otherwise clean dish of sea water. Moreover, small stones of granite, etc., can be activated by contact, for one or two days, with active gravel particles, and these small stones will bring about metamorphosis if dropped into a dish containing swimming larvae. Even sea water which has been standing for some weeks over active shell gravel will by itself induce metamorphosis reactions. The metamorphosis-producing substance can be filtered off from such water, the filter paper used becoming active, the filtered water inactive. Thus *Protodrilus* larvae react, not to the physical nature of the bottom soil, but to some obscure chemical substance which dissolves only slowly in water and is remarkably stable when treated with a great variety of reagents.

In a previous paper (Wilson, 1937) I suggested that larvae such as those of *Scolecolepis*, in which the adult occupies a fairly well-defined zone on the shore, select not merely mud as such but that they are perhaps most strongly attracted to mud inhabited by the adults. I had in mind some sort of chemotaxis to the ancestral home. It has always seemed possible that the larvae of a gregarious species such as *Sabellaria alveolata* (in which, so far as is known, asexual reproduction does not occur), which forms huge honeycomb masses of sandy tubes on suitable shores, may be strongly attracted by the presence of adults or young worms already settled and be induced to settle alongside them. If this be so, it seems likely that the larvae perceive the presence of the adult worms by some sense other than the tactile one. I was thus fully prepared to find that *Ophelia* larvae would show some chemical perception of the sand in which the adults had been living, and some of the experiments were designed to test for this. So far all the results directed to this end have been negative and all positive results have indicated that actual physical contact with the sand, perceived most probably by the tactile sense, is the stimulus to metamorphosis. This stimulus is strongest when the grade of the sand and the shapes of the particles composing it are identical with that of the sand from the Bullhill Bank in which the adults live. The more the character of a sand departs from that of the Bullhill Bank the less readily will larvae metamorphose in it. Mineral composition is probably not so important a factor as shape and size of the sand grains—well-rounded smooth grains, the majority of which pass 40 meshes to the inch but are retained by 86 meshes to the inch, are the main requirement, and the sand must be loose and clean. It is probably not so much the size and shape of the grains which is the stimulus to metamorphosis as the sizes and shapes of the interstices among the grains. It should be remembered that the larvae at metamorphosis are in length one-third to one-half the diameter of the commonest sizes of sand grains present in the Bullhill Bank sand (see Plate XV, figs. 1–3). It may well be, therefore, that smooth rounded grains, each in diameter two to three times the length of the larvae, have among them interstices of sizes and shapes giving degrees of contact with the body of the larva crawling amongst them that induce it to remain there and metamorphose. In other words, if it *feels* right, it *is* right, and the larva seeks no further.

The experiments described in this paper give no indication at all that Bullhill Bank sand, or any of the other sands such as that from Penrhyn Bay which is a moderately efficient stimulus to metamorphosis, contain any slowly dissolving substance that brings about metamorphosis as in the manner of the shell gravel which is active for Jägersten's *Protodrilus*. The indications are, indeed, all against it. The fact that by mixing Carborundum grit with the Bullhill sand metamorphosis is long delayed or prevented altogether is more easily explained on the physical theory than the chemical. So, too, is the effect of cementing the sand in a single layer on the bottom of the dish so that the grains are immovable, though only bedded in the cement on their undersides, leaving most of their surfaces free to release any soluble substances they might contain. It seems that the grains must be movable as well as of the right shapes and sizes; a single layer of grains anyhow will hardly produce interstices comparable to those in a pile of sand. Larvae on surface films just above Bullhill sand hardly ever metamorphose, though they may be there for several days, and the same is true of larvae on the glass bottoms of dishes containing restricted piles of the sand. Larvae are not chemically attracted to these piles but seem to find them by chance contact. Moreover, the finest grades of Bullhill sand, though composed of the same minerals and presumably containing the same, if any, soluble matter as the coarser grains are almost as inactive in a metamorphosis producing sense as are Carborundum grit and sands of sharp angular particles. On the other hand, a proportion, though admittedly a very small proportion, of larvae can be induced to metamorphose by supplying fragments of broken cover-glass or glass wool (Exp. 4), substances unlikely to contain a soluble metamorphosis-producing substance but which might now and again produce interstices of appropriate sizes and shapes which, if found by larvae, would be mistaken for the proper environment. The same remark applies, of course, to the Eddystone shell gravel, gritty sands of angular particles and other unsuitable soils where some of the larvae metamorphosed.

This difference between the reactions of *Ophelia* larvae and those of *Protodrilus* as reported by Jägersten is, of course, in no sense a contradiction of Jägersten's work or of the conclusions he has drawn from it. Neither does my work rule out entirely the possibility of some chemical perception of the grains at close range being employed by the larvae, although it makes such a possibility seem improbable.

Ophelia larvae kept indefinitely under clean conditions or with the wrong kind of substratum either die without metamorphosing or eventually make some attempt to metamorphose. This often consists only in the loss of cilia, but sometimes metamorphosis is successful and more or less normal young worms are produced. Much seems to depend on the health of the larvae at the time, and really healthy larvae seem to last longer without showing signs of metamorphosis than do less healthy ones. In clean dishes the larvae on the bottom as a rule show incipient signs of metamorphosis sooner than do those on the surface film; it is as though contact with something solid does in itself constitute some degree of stimulus quite apart from consideration of shape and size.

The possession by pelagic larvae of the ability to choose the right substratum during a period of time that may amount to several weeks in some species, as in *Ophelia*, is undoubtedly of especially great advantage to those species that are confined when adult to a particular kind of bottom soil, or any other form of restricted type of habitat. It is not intended here to enter fully into the implications on ecological distribution and similar fields of inquiry which this discovery opens up. Points concerning it were made in an earlier paper (Wilson, 1937), and Thorson (1946) has recently discussed the subject at some length and has described some experiments with bottle collectors that 'seem to support the conjecture that marine bottom invertebrates are able to actively choose their substratum' (p. 465).

In the Exe estuary there are a variety of bottoms, some differing widely from the conditions on the top of the Bullhill Bank where *Ophelia* reaches its maximum abundance. The larvae, by their ability to distinguish between the various types and by their selection only of those which are appropriate for adult life, are led to concentrate in the latter and so maintain the normal distribution of the species in the estuary. The pelagic stages will be carried to and fro in and out of the estuary with the tidal currents, and whilst some may be lost out to sea it seems probable that the main swarm does not get dispersed to distant places but remains about the estuary mouth. This must be so, otherwise the species would not be able to maintain itself in that locality, for as far as is known it is not present on outside shores or grounds in the immediate vicinity of the Exe, though full investigation has not yet been made.

Among the grounds over which *Ophelia* larvae will be carried will be the Salthouse Lake area already mentioned. The sand of this area is, as we have seen, generally of a finer grade, more compact and not quite as clean as is the looser sand of the Bullhill Bank. It supports a normal sand fauna with a relatively few *Ophelia* present in some areas. The samples of sand from these areas which have so far been analysed showed a preponderance of grains between the 60- and 100-mesh sizes, but there was a higher proportion of grains between the 40- and 60-mesh sizes than in the Salthouse Lake sample used in the experiments and whose composition is given on p. 735. This latter sand is, as was seen in Exps. 7, 12 and 13, not as effective in bringing about metamorphosis as is the Bullhill Bank sand, and it may be presumed that the rather similar sand from the Salthouse Lake area where a few *Ophelia* may be found (about 12 per m.^{2} as against up to 268 per m.^{2} on the Bullhill Bank, according to Mr N. A. Holme's figures—private communication) would likewise be relatively unattractive to the larvae. If this be so, we have a reasonable explanation of the observed distribution of *Ophelia* in the Exe estuary, a heavy concentration in the metamorphosis-stimulating sand of the Bullhill Bank and the Polesands, with a much lower concentration in the less stimulating Salthouse Lake area. As the larvae in the later pelagic stages drift over the banks the majority of these coming into contact with the Bullhill sand will enter it and stay there, but of those washed over the Salthouse Lake only a small proportion will settle, the majority will leave the sand after testing it and, continuing pelagic life, may later on eventually reach the Bullhill Bank or the almost equally suitable Polesands nearer the open sea. This explanation is at least as reasonable as supposing that there is an even settlement over the whole area followed by greater destruction of the young worms in the unfavourable soils, and the results of these experiments support it.

SUMMARY

Experiments with larvae of *Ophelia bicornis* Savigny have shown that they metamorphose most readily in sand from their natural habitat and with hesitancy or not at all in sands from other sources. Their natural sand consists largely of smooth rounded grains of quartz, very uniform in size; sands of smaller and more angular grains are unfavourable to settlement and metamorphosis. It appears that size and shape of the sand grains, or perhaps, more likely, the sizes and shapes of the interstices among the grains, perceived probably by the tactile sense, is the main stimulus to metamorphosis. Chemical substances dissolving out of the sands do not seem to be responsible for this.

There is a period of time, amounting under favourable conditions to several weeks, during which an *Ophelia* larva is able to settle and metamorphose as soon as it comes into contact with a substratum suitable for adult life.

The ability of the larvae to distinguish bottom deposits suitable for adult life from those which are unsuitable must be of great advantage to the species in maintaining normal distribution and in conserving larvae.

Larvae kept indefinitely in glass dishes without sand, or with a deposit of the wrong kind, eventually either die without metamorphosing or attempt to do so with greater or less success.

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EXPLANATION OF PLATES

PLATE XV

Photomicrographs of living *Ophelia* larvae, × 50.

Fig. 1. Unmetamorphosed larva attached to a sand grain by the anal papillae. The larva is squat in shape and the region of the prototroch is dark and distinct.

Fig. 2. Larva in early metamorphosis crawling on the bottom of a glass dish. The larva is elongating and the dark prototrochal tissues are less distinct.

Fig. 3. Two metamorphosed larvae on a large sand grain; one is attached by the anal papillae, the other is crawling round the grain. The body is longer and the head narrower than before and no dark prototrochal tissue remains. The central portion of the gut is dark and distinct. In the original photograph the long bristles are visible, but are likely to be lost in the reproduction.

Fig. 4. Cluster of about one hundred unmetamorphosed larvae attached to a cotton fragment.

All larvae were from the same experiment and were 13 days old. The cluster was from a clean dish without sand, the others were from a dish containing Bullhill Bank sand. Photographed in July 1948 with electronic flash apparatus using a Mullard LSD 3 flashtube. Duration of exposure about $\frac{1}{3000}$ sec.

PLATE XVI

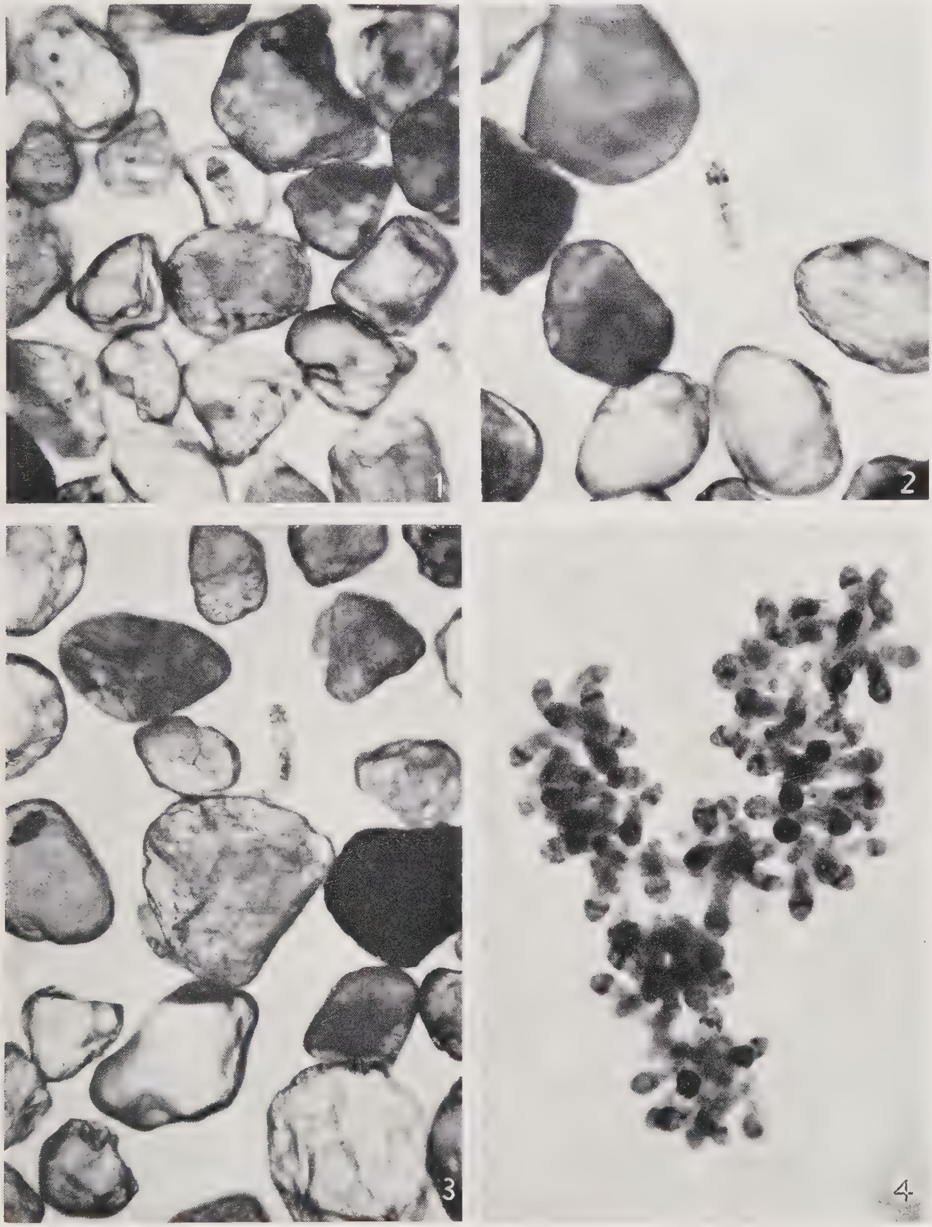
Photomicrographs of sands, × 21.

Fig. 1. Bullhill Bank sand.
Fig. 2. Bullhill Bank sand, 86–100 mesh.
Fig. 3. Salthouse Lake sand.
Fig. 4. Kames Bay sand.

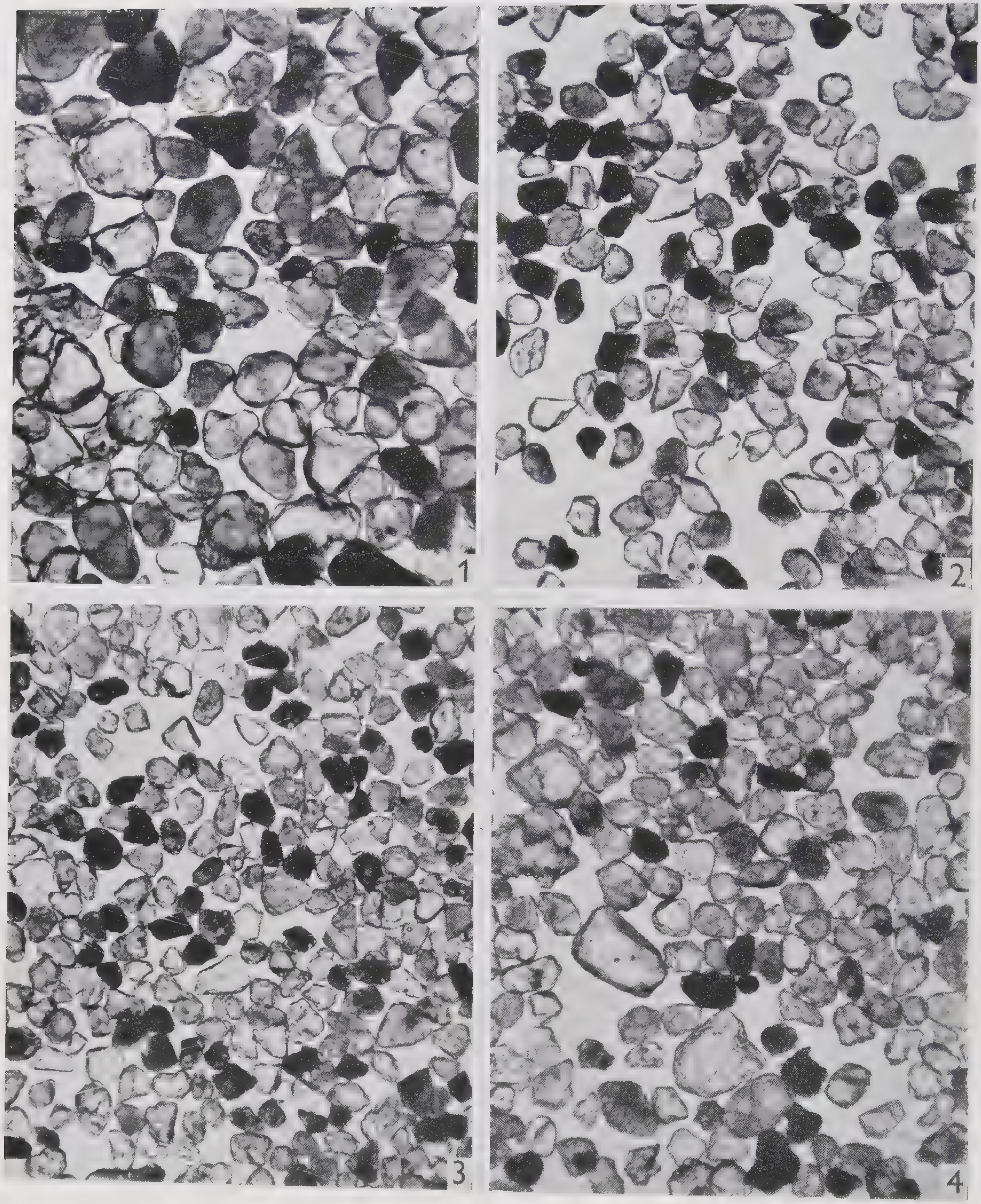
PLATE XVII

Photomicrographs of sands and 'Grits', × 21.

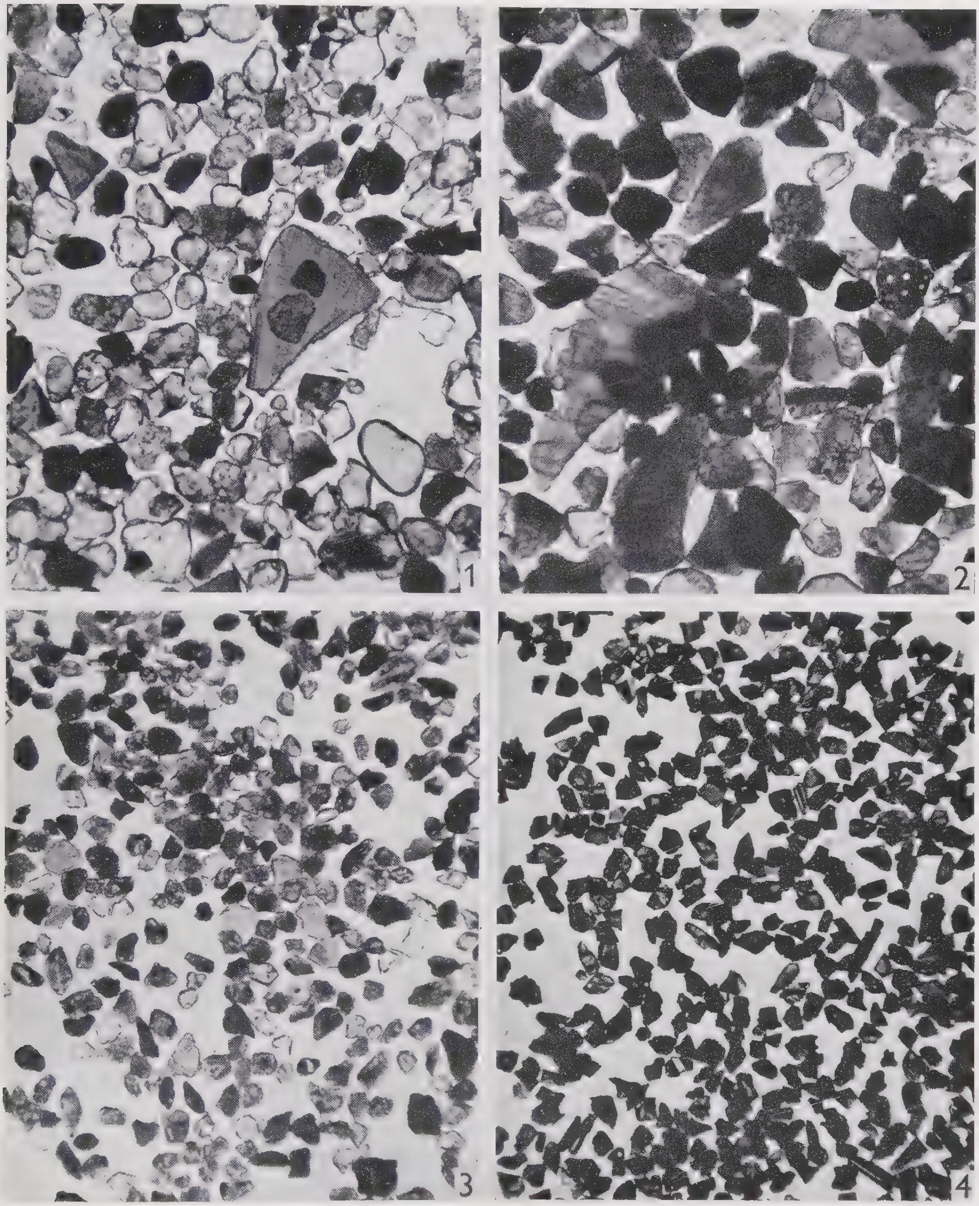
Fig. 1. Penrhyn Bay sand.
Fig. 2. Polzeath sand.
Fig. 3. Fine 'Gritty' sand.
Fig. 4. Carborundum grit No. 120.



Figs. 1–4.



Figs. 1–4.



Figs. 1–4.

THE PLYMOUTH LABORATORY OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM[1]

By F. S. Russell, F.R.S.

Director of the Plymouth Laboratory

(Plates XVIII–XXV and Text-fig. 1)

In *The Times* of 31 March 1884, it was announced that a meeting would be held that day in the rooms of the Royal Society for founding a society having for its purpose 'the establishment and maintenance of a well-equipped laboratory at a suitable point on the English coast, similar to, if not quite so extensive as, Dr Dohrn's Zoological Station at Naples' (M.B.A., 1887*a*). With Prof. T. H. Huxley in the chair a gathering of distinguished gentlemen gave reasons why such a laboratory should be built. All stressed what its value would be from the purely scientific viewpoint, and all were agreed that both by fundamental research and by more direct investigations on our food fishes, knowledge of economic import would be gained. The last speaker, Mr George J. Romanes, said that there was one function of the proposed laboratory which had not received the attention it appeared to deserve; he meant the investigation of invertebrate physiology. 'In the invertebrate forms of life', he said, 'we saw life in its simplest shape, and in the shape which best admitted of observation and experiment, with the view of throwing light upon most of the great questions relating to the processes of life' (M.B.A., 1887*b*).

As a result of this meeting a corporate society, the Marine Biological Association of the United Kingdom, came into being. It was decided that the laboratory should be built at Plymouth where a rich and varied fauna was available. The building, which was opened on 30 June 1888 (M.B.A., 1888), is situated under the walls of Charles II's Citadel in a commanding position overlooking the waters of Plymouth Sound.

The Association, which owed its inception largely to the initiative and energy of Sir E. Ray Lankester, received and still receives financial support from persons interested in the study of biology and the sea, who are the members of the Association. In addition, considerable financial backing was given by a number of Universities and other public bodies, and notably the Fishmongers' Company. From its beginning an annual grant was made by H.M. Treasury, and after the 1914–18 war this grant began to assume considerable proportions when it came under the control of the Development Commissioners.[1]

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[1] This lecture was delivered to the Royal Society on 6 March 1947 (*Proc. Roy. Soc., London*, B, Vol. 135, pp. 12–25, 1947), and is reprinted in this Journal by kind permission of the Council of the Royal Society.

In 1902 the Association was asked by H.M. Treasury to undertake the English share of the scientific investigations which formed part of the programme of the International Council for the Exploration of the Sea (M.B.A., 1903). The English share of these international fisheries investigations was divided under two heads.

I. A survey of the trawling grounds and fisheries in the southern North Sea, together with scientific observations on migrations, feeding and rate of growth of the more important fish. For this purpose the Association also ran a laboratory at Lowestoft.

II. A hydrographic and plankton survey of the western half of the English Channel.

After the 1914–18 war the Lowestoft laboratory 'was re-established under the Ministry of Agriculture and Fisheries for the purpose of studying problems having a direct bearing on the commercial fisheries. At the same time a substantially increased grant was made to the Marine Biological Association for the maintenance of the Plymouth laboratory, so that researches of a more general or fundamental nature concerning life in the sea might be developed on a larger plan' (Allen & Harvey, 1928). The years between the two great wars saw an increased staff at the Plymouth laboratory, and constant additions to the buildings and improvement of facilities for research of all kinds.

Over the period that the Association has been in existence it is possible to trace a sequence in the development of the work from the titles of the many papers in the Association's own *Journal* and its other publications (M.B.A., 1928). It should be remembered that in the earliest days practically nothing was known about the life histories and habits of even our commonest food fishes, and few carefully compiled accounts of the commercial fisheries were in existence. Since the avowed objects of the Association (M.B.A. 1887*b*) were to establish one or more laboratories on the British coasts 'where accurate researches may be carried on leading to the improvement of zoological and botanical science, and to an increase of our knowledge as regards the food, life, conditions and habits of British food fishes, and molluscs in particular, and the animal and vegetable resources of the sea in general', it was only natural that the emphasis in the beginning had to be on fishes. Accordingly, we find that a large number of the earlier papers were devoted to observations on the habits of fishes, shellfish and other products from the sea, and to the collection of information on the methods and results of commercial fishing. This was very necessary, because the few naturalists concerned had to have a general picture of these matters to be able to answer with some feeling of authority the many questions that must have been put to them once the Association was founded.

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[1] An interesting account of some of the early history of the Plymouth laboratory is given by G. P. Bidder (1943) in his obituary notice of Dr E. J. Allen.

I have no doubt that quick results were expected in those days as they still are in certain quarters to-day.

But in addition to doing fishery research, the few naturalists of the staff, together with a number of enthusiastic visiting workers, were building up a knowledge of the marine fauna and flora off Plymouth and its neighbouring coasts. This again was a first requirement, because in all branches of science the systematic observations must come first. More direct fishery research also naturally received considerable attention as a result of the assumption of the English share of the investigations under the International Council for the Exploration of the Sea. But some of the programme of these investigations gave opportunities for increasing the pure scientific observations and studying the environmental factors in the sea over a wide area. Thus much of the foundation was laid for our knowledge of the hydrological conditions round the British Isles, of the fauna of the sea floor, and of the microscopic plants and animals which drift with the water and form the plankton.

Looking back over the first twenty years of the Association's life it is remarkable how much ground was covered by the few research workers available and how well balanced on the whole had been the distribution of the investigations. A most valuable fauna list (M.B.A. 1904, 1931) had been produced, a beginning had been made in the study of the distribution of the animals in relation to their environment, and fishery research had been put on a solid basis. Many papers on the morphology and development of marine organisms had been published, and, in addition, here and there appeared a paper somewhat before its time which gave advanced indications of other possible uses to which the Plymouth laboratory might be put.

After the 1914–18 war there was a noticeable change in the subject matter of the contents of the Association's *Journal*. With the taking over of fisheries research by the Ministry of Agriculture and Fisheries the work at Plymouth became for the greater part fundamental in nature. All the emphasis was on the study of the chemical and physical conditions of the environment, the life histories and development of marine invertebrate animals, and the distribution in space and time of the animal populations. But at the same time the economic aims were not entirely lost sight of and a certain amount of research on the biology of fishes was continued. Such a preservation of a link with more direct fishery research is of value if only because it necessitates that contact shall be kept with current work elsewhere. The Association has, for instance, undertaken research on the breeding and habits of the mackerel, the distribution of seals, the effects of T.N.T. on oysters, and other problems, at the request of the Ministry of Agriculture and Fisheries. But such research should not nowadays be needed as a justification for receiving a Government grant. All fundamental researches in the long run justify themselves, and the bulk of the work done at Plymouth is essentially fundamental in nature.

Thanks to the valuable work of the Fisheries Departments our factual knowledge of the important food fishes is such that the populations of fish on which our food supply depends can now be watched with a view to the regulation of the catches. The major picture of the distribution, migrations, growth and spawning habits of the common fish is now well known. But what the underlying factors may be, on which the fishes' lives and habits depend, remain to a large degree unsolved, and their solution lies more in the realms of pure science. It seems likely, therefore, that all fisheries research will become more fundamental in nature and aimed at understanding the great natural fluctuations in the fish populations and the causes of the habits of the fish themselves.

It may be noted that most of the researches that have been undertaken in recent years by the staff of the Plymouth laboratory can be built around two main underlying themes. The first is how much living matter can the sea produce, what are the variations and causes of variation in productivity, and how do the organisms obtain the materials necessary for life? The second is how do marine animals in general live, how do they fit their various individual environments, and what alterations in the conditions in their environment can they appreciate? Both require a knowledge of the physical and chemical conditions in the sea. Where the productivity of the sea is concerned the sea water is the medium which contains all the ingredients necessary for the successful growth and development of the living organisms; in so far as the general biology of the animals is being studied it is the conditions in the sea water which determine their distribution, habits and migrations.

The Plymouth laboratory is therefore equipped for studying the physics and chemistry of the sea. Researches of the staff are aimed at the development of methods for estimating the quantities of nutrients in the sea water upon which the unicellular plants depend and following the changes they undergo throughout the year and from place to place in relation to the plant crop. The approximate yearly cycle of the more abundant constituents, phosphorus, nitrogen and silicon is now known. But much remains to be done in studying their rate of turn-over, and long-term investigations have shown periodic fluctuations in the amounts available. This is now being linked with hydrological observations on the movements of water masses and their origins, for much will depend upon whether the water is drawn from the rich deep ocean layers upwelling on the continental shelf or from the more depleted surface waters.

One of the first necessities in this research is a knowledge of the amount of photosynthesis; photoelectric methods have therefore been adapted for the measurement of the penetration of light into the sea, and the extinction by absorption and scattering of its component wave-lengths at varying depths.

In order to solve some of the problems thus posed it is necessary to work with pure cultures of diatoms and flagellates, and for many years attention has been given to this side of the work. Advances have thus been made in our knowledge of the utilization of combined nitrogen and phosphorus by the plants, these constituents often being present in such exceedingly low concentrations in the sea as to limit plant growth. Research is also being made on other substances, necessary only in minute quantities as trace elements, now known to play a vital part in the growth of land plants. Thus the concentration of both iron and manganese is probably suboptimal in some waters and may indeed limit plant production.

It is on the production of these unicellular plants that all the animal life in the sea depends, and ultimately those fish which form so valuable a part of man's food supply. The first link in the chain from plant to fish is the minute animal life of the plankton. Not only are these eaten directly by such fish as the herring and the mackerel, but they are of direct importance to nearly all species of fish, because when first they hatch the young fish are too small to eat anything larger. Researches on distribution, abundance, growth and habits of the many species of animals in the plankton therefore form a necessary part in the general problem of productivity. The effects of grazing off the plant crops by these animals can be studied at sea by evaluation of their numbers in measured volumes of water, and in the laboratory by experiments on the rate the animals eat the plants when cultured.

Observations on the distribution of the plankton organisms are made also in connexion with the hydrological surveys. It is found that some species are restricted to certain types of water, and they can thus be used as indicators of their respective water masses. Some waters in the Plymouth area, which are thus clearly characterized biologically, are not readily distinguishable by the usual hydrological features such as salinity and temperature. Such biologically distinguishable waters may differ markedly between one another in the amount of life they carry. This must in turn be related to their chemical content.

Other links in the chain are the bottom animals upon which the growing fish feed. It is necessary first to know the distribution of these animals. The bottom deposits of the sea are not uniformly distributed, ranging as they do from the finest mud to the coarsest gravel according to the movements of the overlying water. Each kind of deposit has its characteristic fauna; and recent researches have shown that the microscopic larval stages of some animals will only undergo their normal metamorphosis if they can find the individual grade of soil they live in. The estimation of the food available in different deposits has received attention, and attempts have been made to evaluate the animal contents of standard samples of deposit.

There is another link in this productivity chain whose connexion may not at first appear obvious. Quite early in the history of the Marine Biological Association the opportunity was taken, while studying the distribution of bottom animals, to examine also the stones and rocks dredged up in order to throw light on the geology of the English Channel. A knowledge of the configuration of the sea floor is of importance for the study of water movements. The shape of the continental edge where it passes over from the shelf to the steeper continental slope may be of critical importance, for it is here that the deeper waters of the ocean, rich in nutrient salts, are brought towards the surface at times by upwelling and reach the photic zone. It may well be that embayments resulting from submerged valleys may cause submarine waves to increase their amplitude and thus reach higher levels.

Let us now consider the second major line of research, the biology of marine animals. Every species of animal in the sea can form a subject for enquiry, and each alone can pose nearly all the problems of biology. The sea provides a greater variety of animals than any other environment. In it are to be found representatives of all the groups of the animal kingdom, the insects alone being scarcely represented. Many groups indeed are found almost exclusively in the sea. The facilities offered by the Plymouth laboratory therefore afford an inexhaustible mine for any biologist, and it becomes difficult to canalize the work into any single objective line. There is scope for systematists, for morphologists and embryologists, for students of life histories and behaviour, for geneticists and so on. In general it may be said that, once the ground has been laid open by the systematists, research has chiefly been directed towards the description of the life histories of animals important in the general economy of the sea, of their food and methods of feeding, of their breeding and rate of growth, their parasites, and of their relationships with their animate and inanimate environment. Many of the results of investigation obviously have also a bearing on the general problem of productivity. In this wide field for research the emphasis tends to vary from one direction to another according to the predilections and aptitudes of the individual workers, but, apart from their value as contributions to general biology, any one of them can be shown directly or indirectly to have its practical bearing. Knowledge of the life histories and habits of fishes in general has obvious value, even where species of no commercial interest are concerned, since they are all competitors for the common food supply. Very useful results have accrued from investigations on the herring, which at one time formed an important winter fishery at Plymouth, attracting a hundred or more steam drifters from the east coast ports. In the early 1930's the herring ceased to come in their usual numbers to the grounds near Plymouth, and it became possible by local observations to warn the industry of the reduced chances of a successful fishery and thus save the considerable expense of sending ships to the area. The causes of the disappearance of the herring are, however, of the greater fundamental interest and the answer may be found when our knowledge of water movements grows.

Apart from the more obvious necessity of research on the biology of crabs, oysters, mussels and other shellfish used for food, knowledge gained about invertebrate animals in general has proved its worth. The annual cost to the nation resulting from damage to underwater structures by boring organisms and by the fouling growths on ships' bottoms is immense. All attempts to reduce this wastage by improved methods require at the start a knowledge of the natural history of the organisms concerned. Other departments are now taking up antifouling problems, but they begin with a basic knowledge already supplied by fundamental researches.

It is not wise in the long run to restrict observations only to those organisms known to be of economic interest. It has been noteworthy that our common coastal seaweeds attracted little attention in the past. In relation to the general economy of the sea as a whole the narrow fringe of weeds around our coasts is of small importance; probably largely for this reason the seaweeds were neglected. But during the war, when supplies of certain raw materials were cut off, seaweeds were needed as a source of supply of alginic acid, agar and mannitol. It was then realized that we knew practically nothing of the rate of growth and breeding of our commonest weeds, and investigations were immediately begun.

I think this necessity for the accumulation of knowledge without regard for its immediate practical value should be stressed, for it has proved itself abundantly worth while. The Association has often advised Government departments with resulting savings in expense. A knowledge of the effects of temperature on the rate of growth of marine organisms was incidental in the destruction of fouling organisms and their prevention for many succeeding years in a large basin in one of our naval dockyards. And, in passing, it is worthy of mention that research on the preservation of ropes and nets, besides enabling the Plymouth laboratory to make considerable economy in the use of expensive silk plankton nets, resulted in great saving for the Ministry of Home Security when proven methods were adopted for preserving sand bags.

But marine animals live not only in the open sea. They inhabit the intertidal zones of the shore and they invade the estuaries. Work cannot therefore be limited to offshore waters; the shores and estuaries must also receive attention. The examination of the estuarine fauna is of great interest physiologically, and a detailed knowledge of the distribution of the different species in relation to the normal changing conditions is of value in assessing pollution. As a result of a close study of a water shrimp (*Gammarus*), primarily as a subject for genetics, certain species are proving to be valuable estuarine indicators.

From the point of view of life in the sea as a whole it should be realized that work at Plymouth touches only the borders of the great oceans, whose study lies within the province of the highly organized oceanographical expeditions. Nevertheless Plymouth plays its part in the promotion of oceanographical research. This is especially so in the development of methods. Many of the methods used on ocean-going expeditions have been developed at Plymouth. This is an essential part of the laboratory's work. Once an oceanographical expedition is equipped and its programme planned it is necessary that the majority of the observations should be carried on by routine methods, for results lose comparative value if they are constantly varied en route. At Plymouth, however, there is full opportunity to develop methods in the laboratory and test them out at sea. Each succeeding cruise by the ocean-going research vessels may therefore take advantage, and employ the improved methods and attack new problems for which the necessary technique had been awaiting development at a shore laboratory.

This brief review of the problems open to investigation shows some of the field of research available to the Plymouth staff. The scientific staff is small, only a dozen or so in number. The most that can be done is to distribute this staff in a balanced manner so that there is one engaged in each of the possible major lines of inquiry. Some might argue that it would be better to concentrate all the energy on to one specific problem. This could only be done by the formation of a school and the interests of the leaders of this school might determine a one-tracked course for many years.

This should never be at Plymouth, because there is another most important side of the laboratory's work upon which I have not yet touched. It has been a tradition of the Plymouth laboratory that it shall attract visiting research workers. The constant flow of visitors gives life to the buildings and, with its ever changing interests, affords invaluable points of contact for the staff. It is essential, therefore, that the interests and experience of the staff should cover as wide a field as possible so that visitors may receive assistance and mutual benefit be derived.

The additions to scientific knowledge produced by the many visitors must exceed those of the staff itself and they are for the most part published in journals other than that of the Association. Much of this work has been on traditional biological lines, but it may be noted that, even on the day of the Association's foundation, the words of Romanes pointed to other fields. When the time was ripe the scope was broadened to include the comparative physiology of marine animals. In this direction Plymouth has always been understaffed, but it has for long been the aim as far as space will allow to equip the building with the necessary facilities and apparatus so that visiting workers may fill this gap.

The physiological researches made at Plymouth have been very varied, and mention only can be made here of some of the subjects which have received attention. The common spider crab (*Maia*) has been much used for studying the heat formation in nerves and other problems of the physiology of nerves; the same animal also supplies material for the study of the respiratory blood pigment, haemocyanin. The sea urchin (*Echinus*) has been a fruitful animal for experiments on fertilization and development since its eggs are most suitable in nature. Advances have been made in our knowledge of the nervous coordination of the movements of fishes and on the physiology of the regulation of their colour changes. The functions of the lateral line system in fishes have been partly elucidated, and our knowledge of the labyrinth has been advanced owing to the unique suitability of the dogfish (*Scyllium*) as a subject for experiments.

Nervous systems in their simplest form have been studied in the sea-anemone, and in recent years the squid (*Loligo*) and cuttlefish (*Sepia*) have received prominent attention because they possess giant nerve fibres on which much can be done which is not possible with other nerve fibres; these giant fibres are also to be found in other marine animals, notably some polychaete worms and Crustacea.

Much remains to be done on the physiology of marine animals, and one direction perhaps in which our knowledge is especially lacking is that of the sensory perceptions and environment of animals in the sea.

From these few examples it can be seen that the practical benefits resulting from the founding of the Marine Biological Association may have a wider application than is expressed in its original aims, for these physiological researches have a very definite connexion with the medical sciences.

In this account I have omitted to mention by name the many distinguished men of science whose researches have resulted in the success of the Plymouth laboratory, and who, together with the Association's many devoted benefactors, have raised the laboratory to its present position of world repute. I cannot, however, let the occasion pass without reference to the late Edgar Johnson Allen who, as Director for 42 years, was the guiding genius to whom the Marine Biological Association owes so much of its success (Bidder, 1943; Kemp & Hill, 1943). It is interesting to recall Dr Allen's published works. These were comparatively few, but it is noteworthy that they touched on nearly all the main fields of research covered by the laboratory. To him was due the pioneer work on the culture of diatoms which made possible the great advances in our knowledge of the productivity of the sea. He produced the first important publication on the bottom fauna with his work on the Eddystone-Start grounds, and he was an acknowledged authority on the systematics of polychaete worms. His writings cover many problems concerning fish and other products of the sea. He co-operated in work on development and heredity, and had a deep interest in evolution; and it is perhaps significant that his first researches were on the nervous system of Crustacea. I think this is sufficient to show why the Plymouth laboratory never developed into a one-sided institution.

It would be unfitting also if I failed to include the name of the late Director, Stanley Kemp, whose death came as so tragic a blow just as the war was ending (Hardy, 1946). Dr Kemp's name will go down in history as that of the leader of one of the greatest oceanographical expeditions of all time. The *Discovery* Expedition has become a living institution, and the loss of Dr Kemp is deeply felt by all biologists and most by the staff of the Plymouth laboratory.

I should like also to record one name out of those of the Association's many benefactors, that of George Parker Bidder, for whose wisdom, generosity, and unfailing help in times of need we shall always remain in debt.

The laboratory is managed by a Council of elected members and annual Governors appointed by certain governing universities and other bodies, including the Royal Society, which have given sums of £500 or more. A number of Universities also contribute to the Association by renting tables to which they can nominate research workers. All foreign visitors are welcomed as guests free of charge and every year sees an increasing number of foreigners coming to Plymouth to work and discuss common interests with members of the staff.

The private sources of income of the Association are from these grants and donations, from membership subscriptions and the proceeds of the sales of specimens, collecting gear and journals. By far the largest contributor at the present time is the Government which voted an annual maintenance grant last year of over £25,000. The grant is sanctioned by H.M. Treasury as a draft from the Development Fund, and the Association is deeply in debt to the Development Commissioners, their advisers, and their Secretary, E. H. E. Havelock, for the wisdom and foresight they have always shown in their recommendations for the laboratory's support.

The Laboratory is built of Devonian coral limestone of which the Plymouth Hoe is formed, and marine animals of a past age are clearly visible in the weathered stone. It is not very large; accommodation is restricted by the limited area available between the Citadel walls and the road. It consists of a main south building with the two upper floors divided into working rooms in which about twenty-four workers can be accommodated. Connecting with it is a north block containing the chemical and physiological laboratories. Underneath are cellars excavated from the solid rock which, on account of their uniform temperature and freedom from vibration, are most suitable for research requiring very delicately adjusted apparatus. There is a small constant temperature building with two compartments for controlled low temperatures.

The north block can take about sixteen research workers. The whole laboratory can thus accommodate some forty people[1] at one time, although this number can always be increased by a little 'crowding up'. The present permanent scientific staff numbers twelve, and there are also usually half a dozen or so investigators on long-term grants of a year or more duration. Over and above these about twenty visiting research workers can therefore be accommodated at one time, and it is of course normal for the laboratory to be especially crowded during the summer months when University staffs are on long vacation and visitors come to this country from abroad.

[1] The eastern block of the south building, which was the Director's house, was gutted by fire in a bomb attack. It is being rebuilt as a laboratory and should increase the working accommodation by ten rooms.

There is a valuable library, which is probably the most complete in the country in publications concerned especially with marine biology and oceanography. The library also takes a number of other periodicals likely to be needed by visiting research workers. Many visitors remark on the pleasure of using a library of so compact a nature and with such careful selection of publications.

On the ground floor of the main south building there is an aquarium which is open to the public. Apart from its educational value for the many adults and children who visit the aquarium, the tanks with their living exhibits are a never failing source of interest to the research worker on the habits and behaviour of animals. The exhibits are restricted to the local fauna and provide a representative view of the chief fishes and larger invertebrates of the district.

The tanks, the largest of which is 30 ft. 6 in. long by 9 ft. wide, with a depth of water of 4 ft. 6 in., are supplied from two reservoirs each holding 50,000 gal. of sea water. This sea water which supplies the aquarium is also led to certain parts of the laboratory where small experimental tanks and seawater circulation benches are available.

A subsidiary, but nevertheless vital, function of the laboratory is the part it plays in the general training of biologists. Facilities are provided for courses of instruction during the Easter vacation to university students and schools, who have unrivalled opportunities for seeing at first hand the variety of living organisms which abounds in the sea, and for studying the different environments in which they live. There can be few universities in this country whose zoology staffs do not contain a sprinkling of those who have passed some of their time at Plymouth, either as Easter Course students, members of the scientific staff, or visiting research workers. This is most important in view of the overwhelming preponderance of animal types in the sea.

From time to time more specialized courses are given for post graduate students on the physiology of marine animals, and other special subjects. Plymouth also plays another part in education by supplying to universities and schools preserved and living specimens necessary for teaching purposes.

In order to enable the demands of these manifold activities to be met the Association runs two research vessels (Plate XXIV).[1] The smaller of these, a 25 ft. motor boat, the *Gammarus*, is used for dredging and trawling in waters close inshore, and for visiting the shores at different points for collecting intertidal specimens. The larger, at present a 90 ft. motor fishing vessel (R.V. *Sabella*) on charter from the Admiralty, works in offshore waters. As well as making collections generally for those working in the laboratory, for stocking the aquarium, and for the specimen trade, the first call on this vessel is naturally for research at sea. It is from this ship that quantitative observations are made on the organisms of the plankton and the sea bottom, and from which

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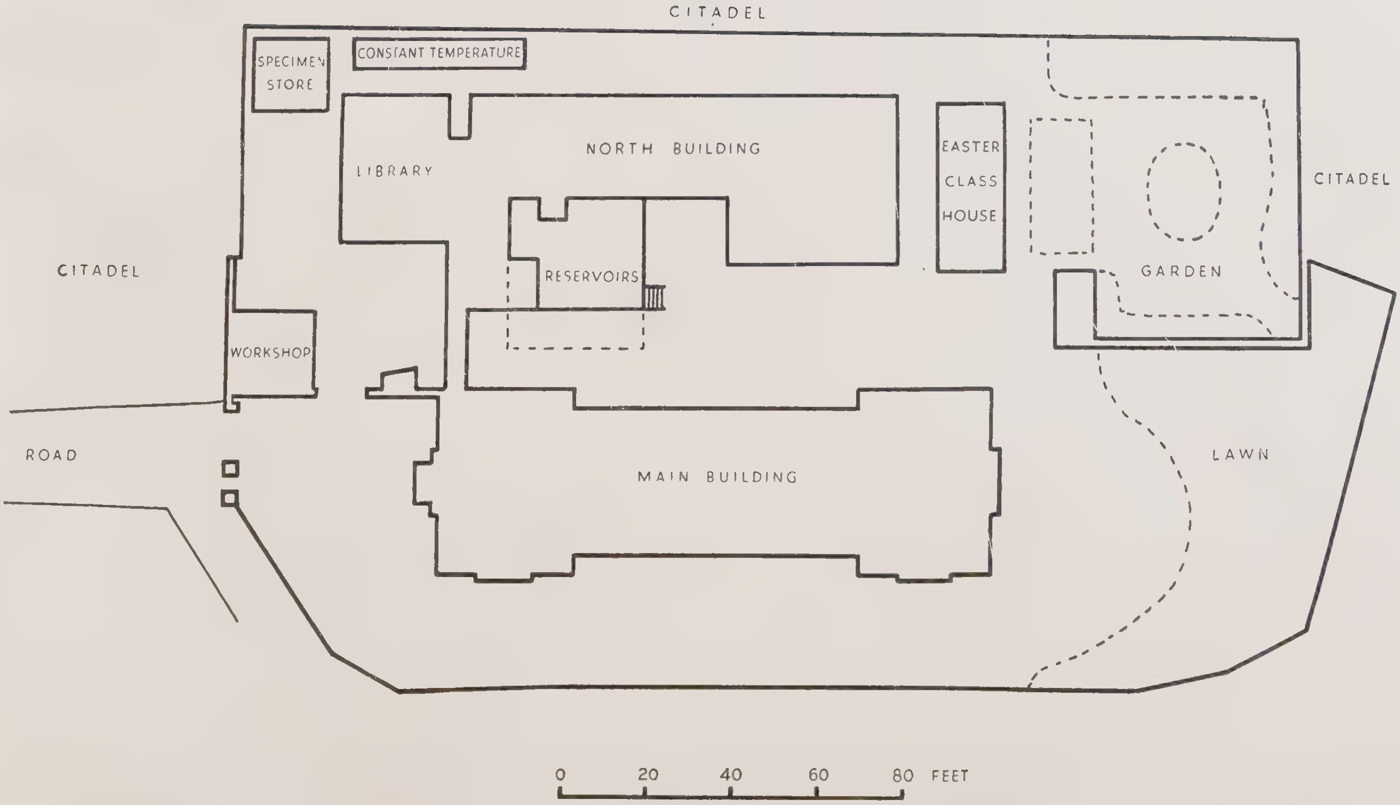
[1] Since this lecture was first printed the Association has purchased a third research vessel, a 61½ foot motor fishing vessel, the *Sula* (Plate XXV).


CITADEL
SPECIMEN STORE
CONSTANT TEMPERATURE
LIBRARY
NORTH BUILDING
EASTER CLASS HOUSE
CITADEL
GARDEN
CITADEL
RESERVOIRS
WORKSHOP
ROAD
MAIN BUILDING
LAWN
0
20
40
60
80 FEET

Text-fig. 1. Site plan of the laboratory buildings.

physical and chemical investigations are made at sea. The ship also makes periodical cruises farther afield to study the hydrology over a larger area including the western approaches to the English Channel.

I hope I have said enough to give some idea of the general activities of the Plymouth laboratory and the possibilities it affords for work. One might sum it up by saying that it aims to give facilities for any research, not necessarily only biological, on problems for which the sea can provide the materials or the environment required. Its position is unique, lying as it does between the extremes of a fishery research laboratory and of an oceanographical institution, yet serving both, and at the same time offering facilities for visitors like the laboratory at Naples on whose pattern it was first founded. Let us hope it may be allowed to continue to hold this focal position and attract all those interested in the science of the sea and indeed of life itself.

Note. There have been extensive alterations to the Plymouth laboratory since the account written by Allen & Harvey (1928). A new library was built in 1931, and in 1932 the north block was farther extended to the eastward, to give increased accommodation for physiological and chemical laboratories, and improved photographic darkroom facilities. A small constant temperature building was added in 1938. In 1939 the centre of the south building, the original main laboratory, was completely renovated and a new floor added. A site plan as at the present date is shown in Text-fig. 1.

I wish to thank Miss E. J. Batham, Mr D. P. Wilson and Mr G. A. Steven for permission to reproduce the photographs.

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EXPLANATION OF PLATES

Plate XVIII

View of the Plymouth Marine Biological Laboratory, taken from the Smeaton Tower on the Hoe looking eastwards towards the Cattewater (summer, 1946).

Plate XIX

Fig. 1. Tank room on the first floor of south building (south side).

Fig. 2. Tank room on first floor of south building (north side).

Plate XX

Fig. 1. Museum on second floor of south building

Fig. 2. Typical work room in south building.

Plate XXI

Fig. 1. Reading room on first floor of library.

Fig. 2. Corner of physiological laboratory.

Plate XXII

Fig. 1. Chemical laboratory.

Fig. 2. Yard between north and south buildings showing reservoirs for sea water on left, outside tanks and circulation bench on right, and end of Easter Course building in distance on left.

Plate XXIII

Fig. 1. General view of aquarium.

Fig. 2. Anemone tank in aquarium.

Plate XXIV

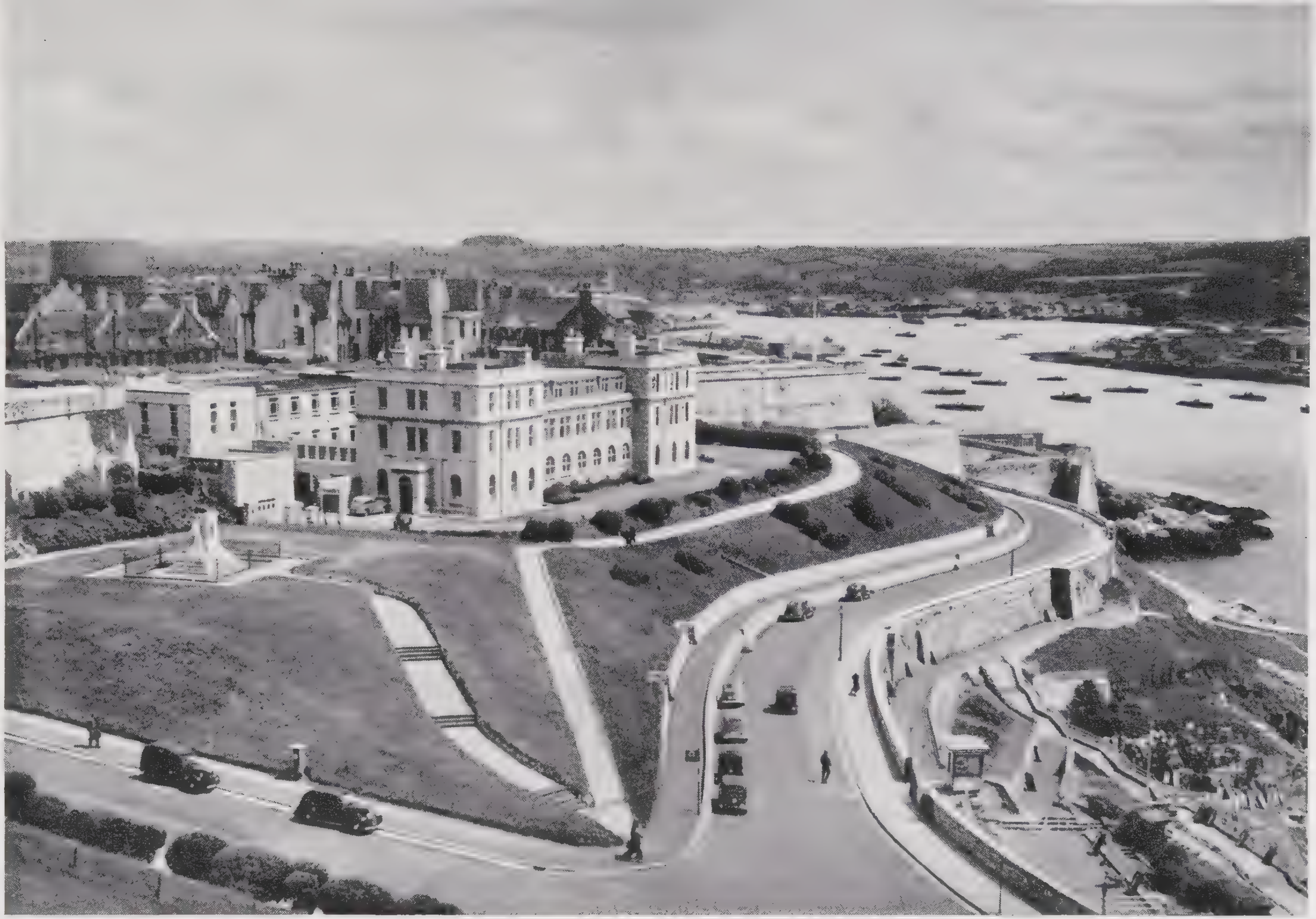
Fig. 1. R.V. *Sabella.*

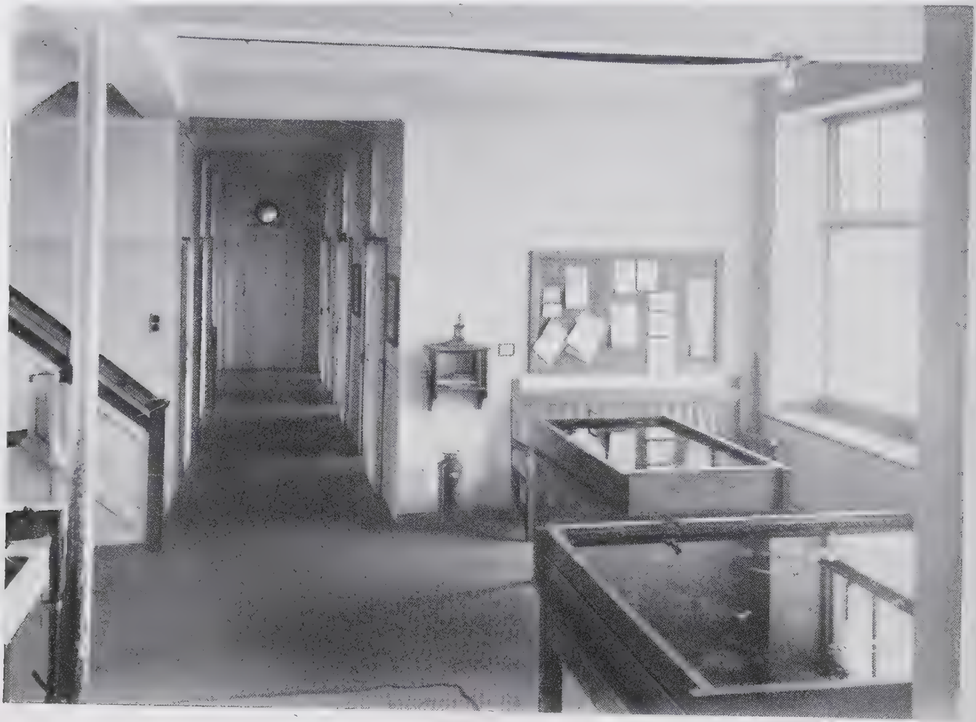
Fig. 2. Motor Boat *Gammarus.*

Plate XXV

M.V. *Sula.*

The photographs for Plates XVIII and XXV were taken by Miss E. J. Batham. All the other photographs are the work of D. P. Wilson, except Pl. XXIV, figs. 1 and 2, which were taken by G. A. Steven.





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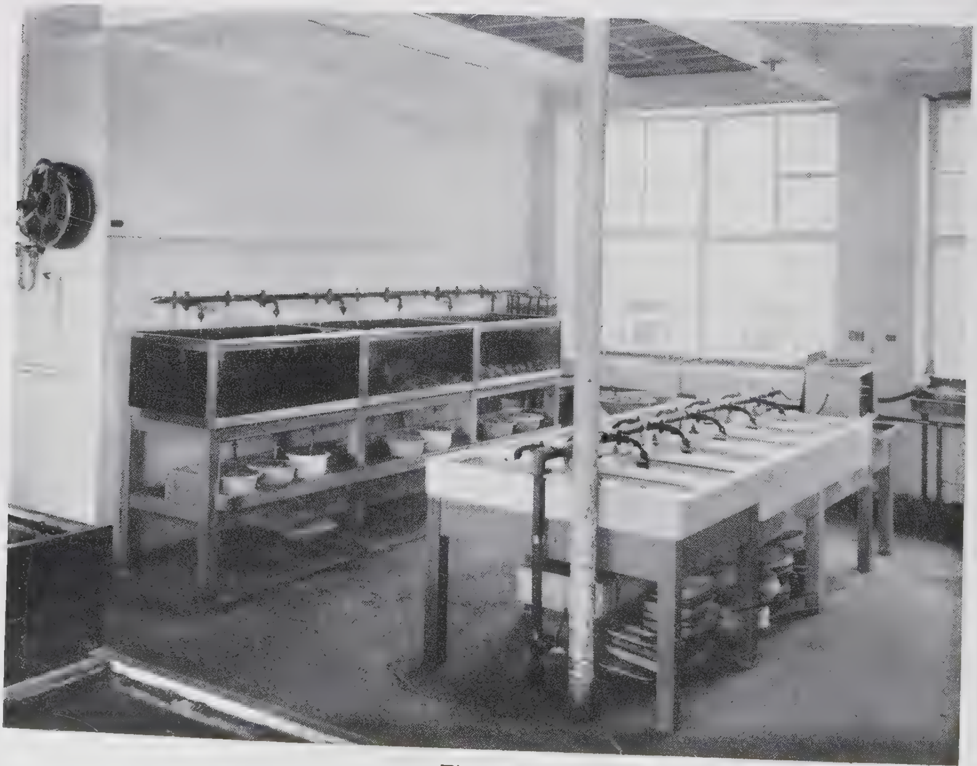

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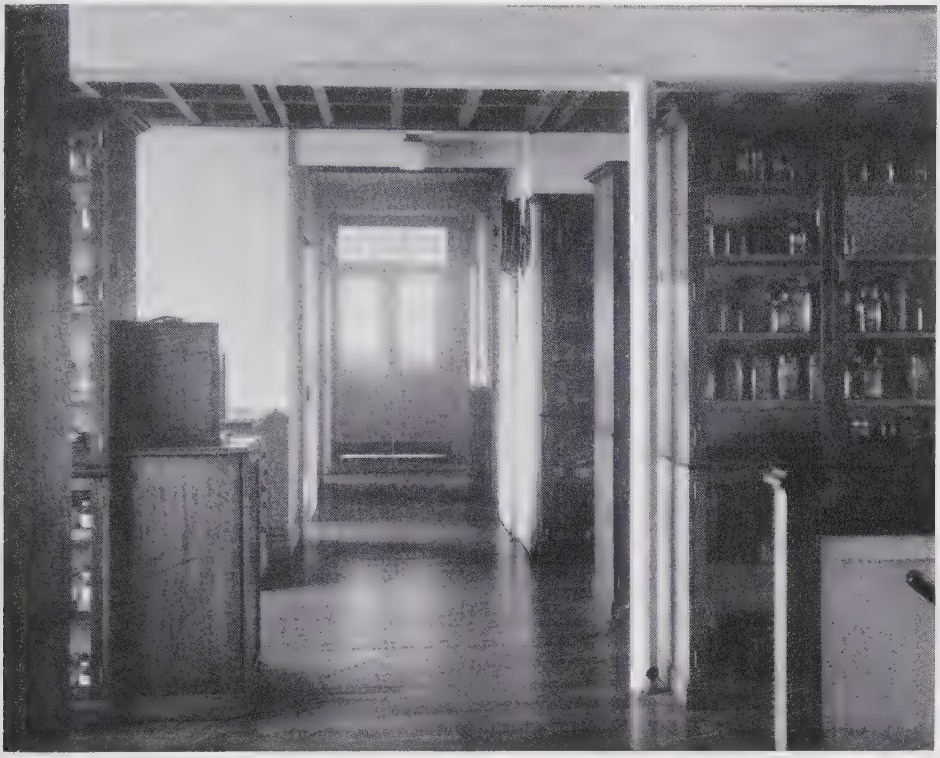

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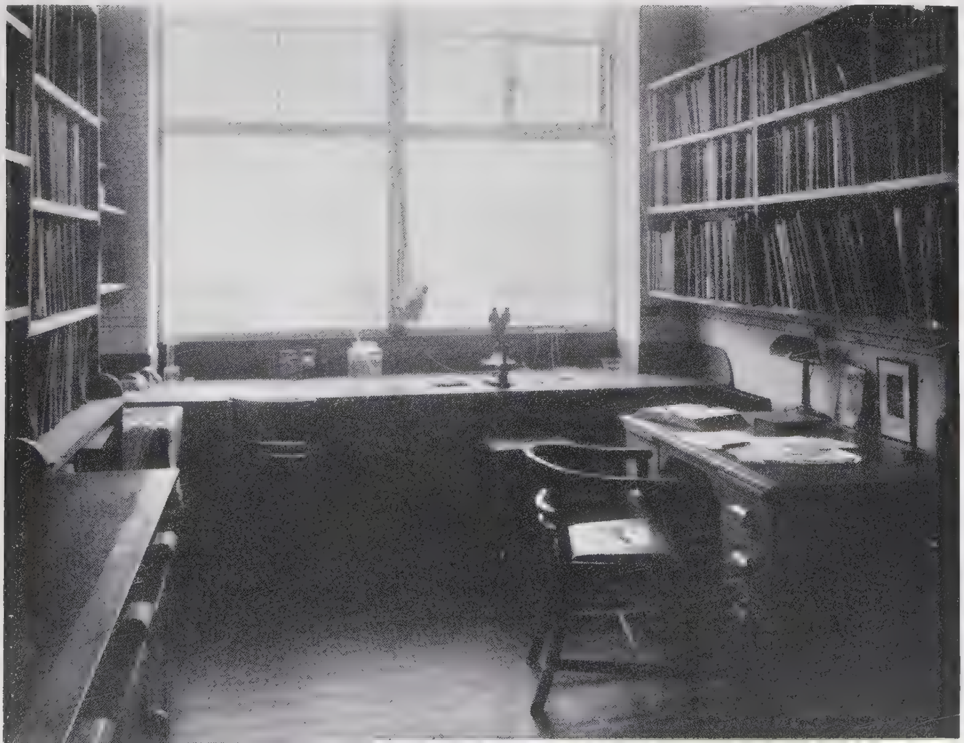

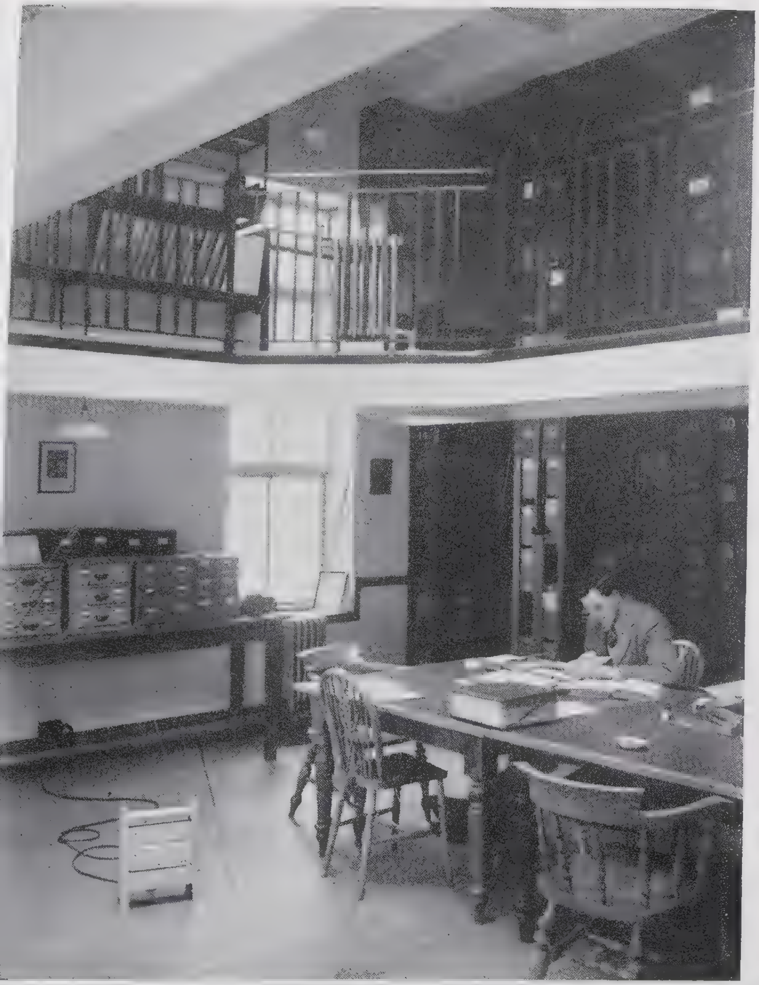

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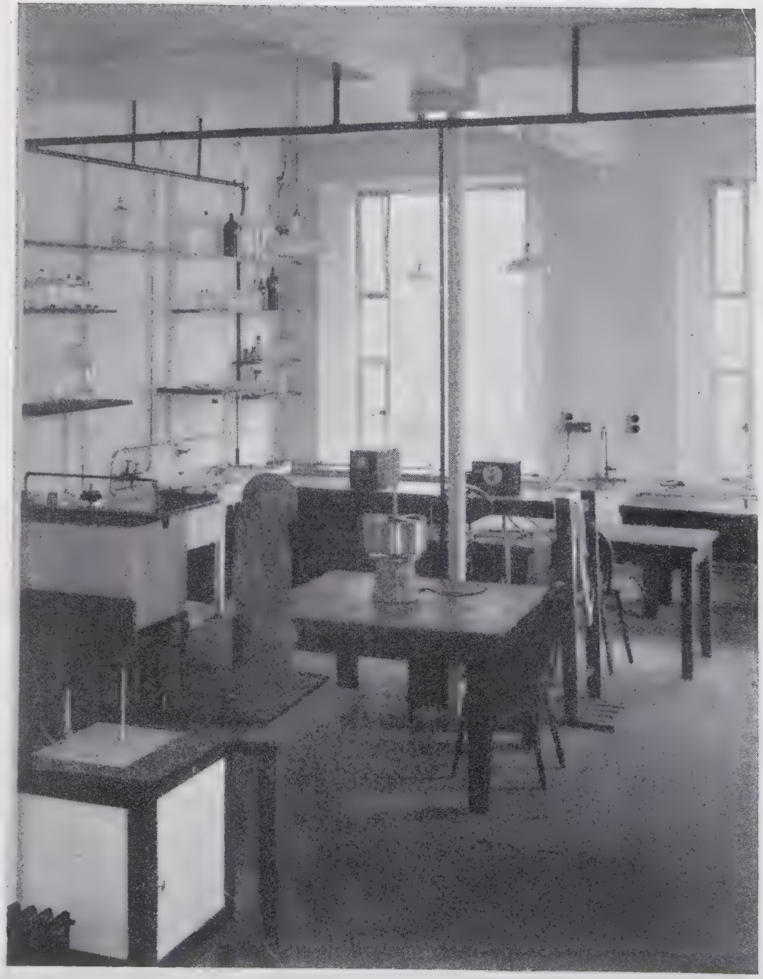

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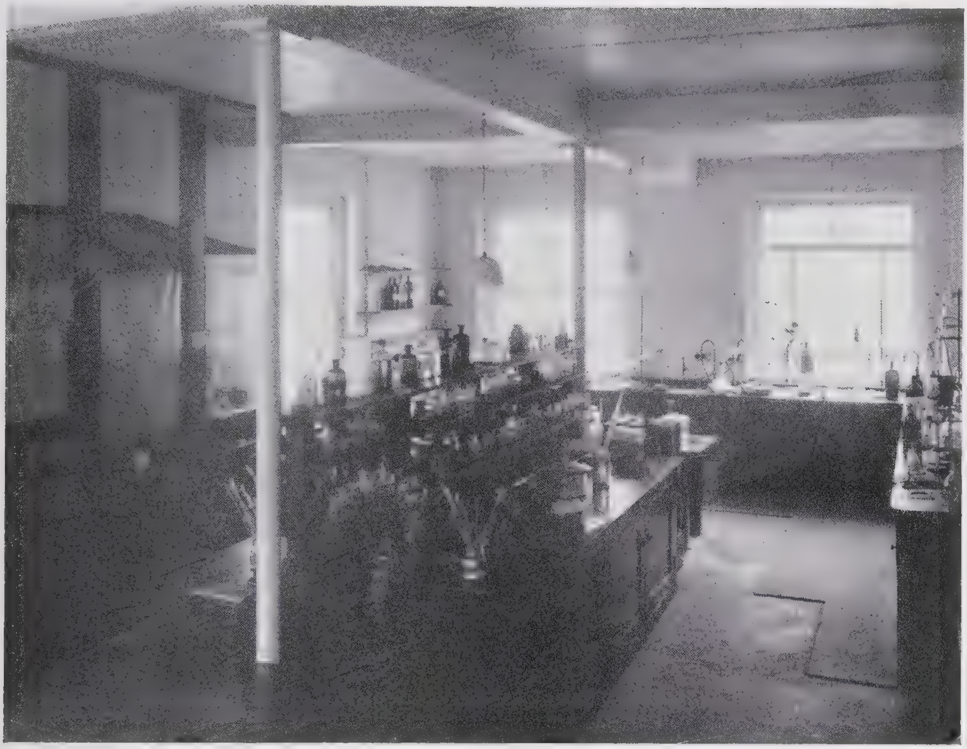

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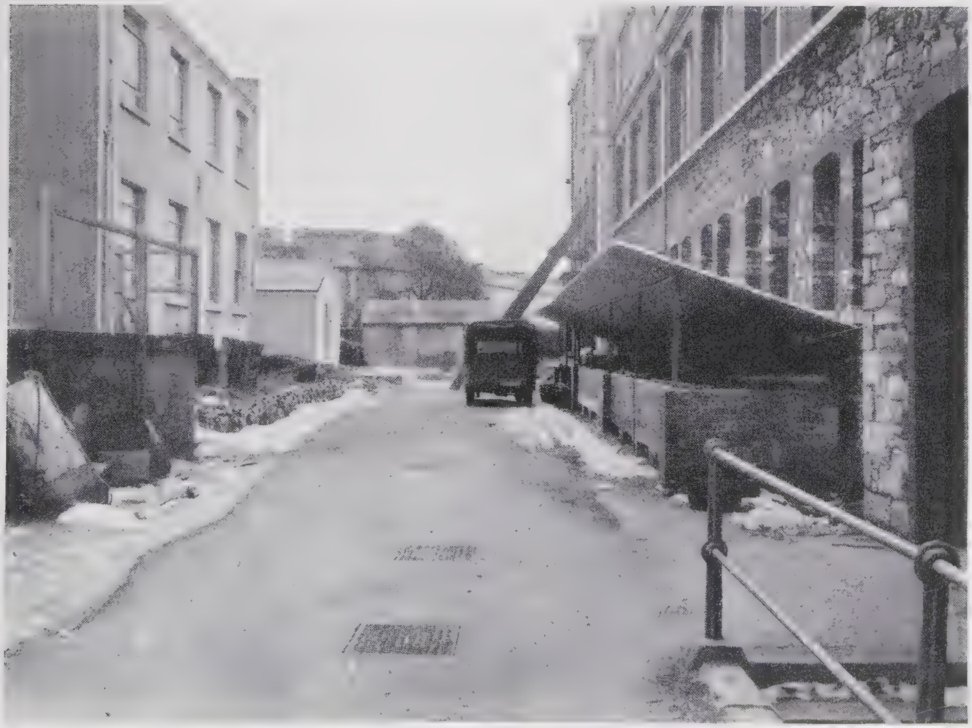

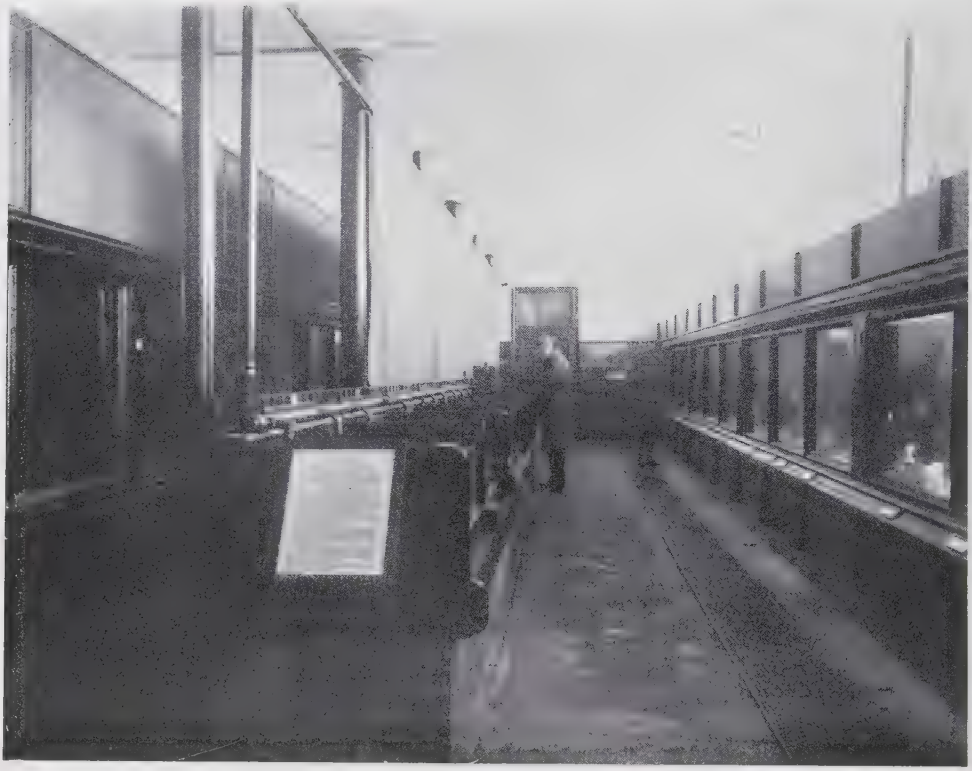

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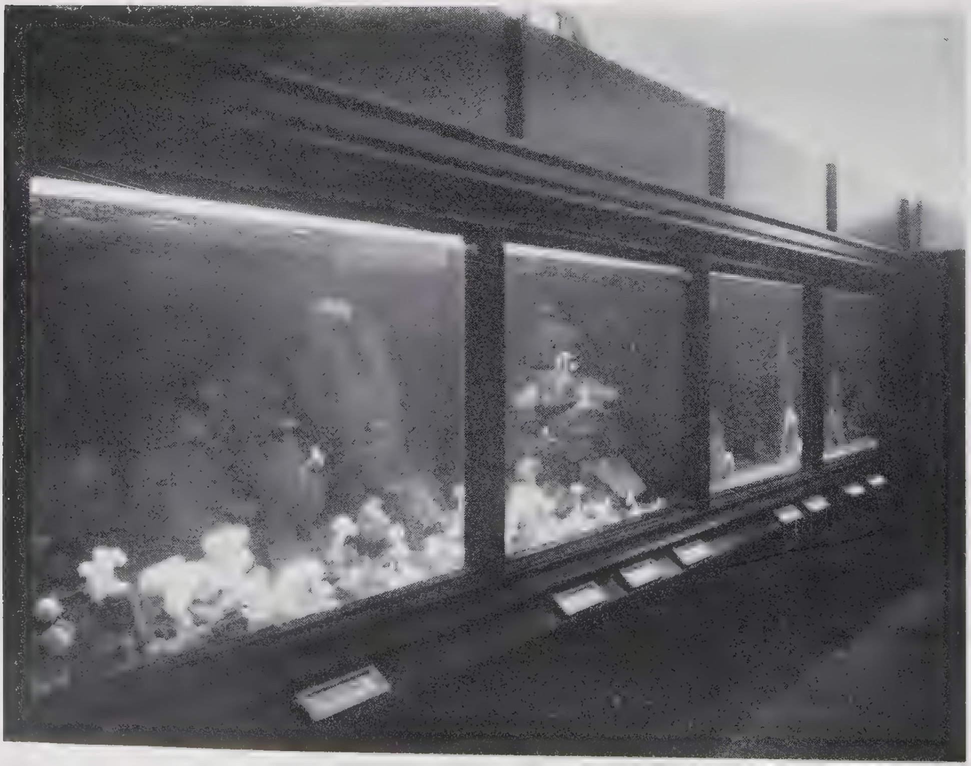

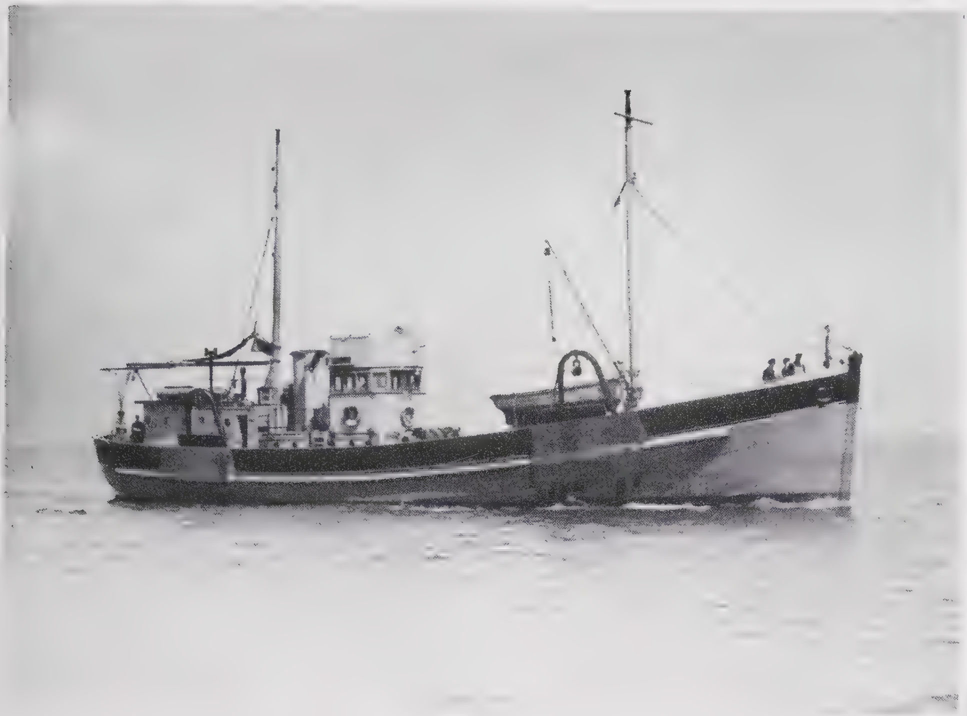

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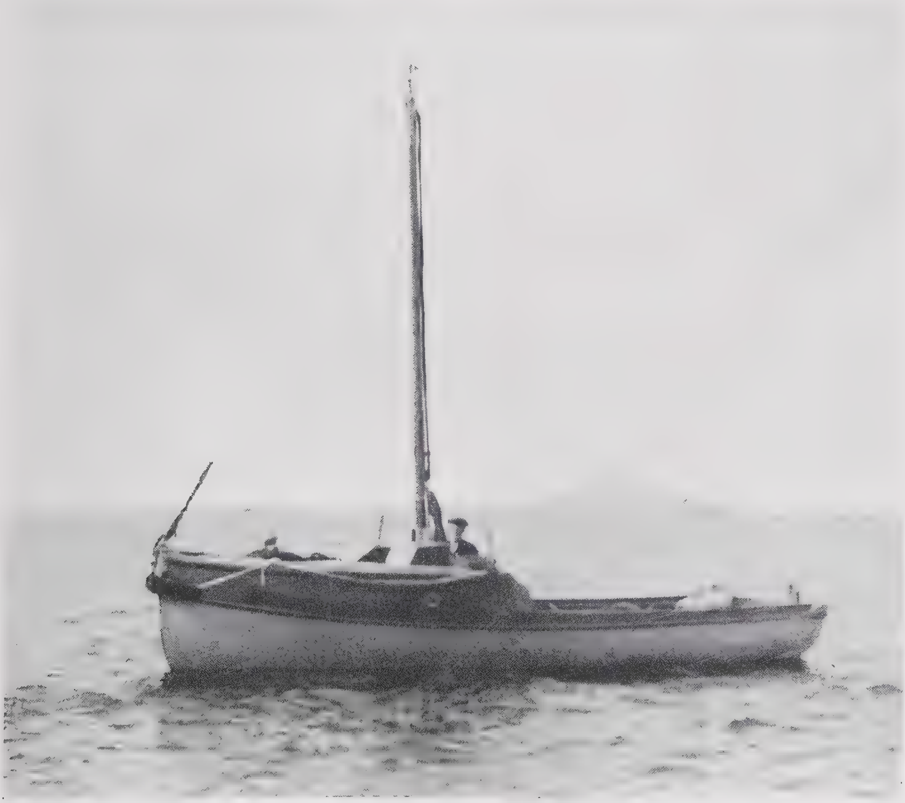

Fig. 2

PLATE XXV

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

GALATHEA

By **Richard B. Pike**

L.M.B.C. Mem. XXXIV, *L'pool*, 1947, *pp.* 1–179, 20 *plates*

This work follows the usual form of the *L.M.B.C. Memoirs*, giving a fairly complete description of the external and internal anatomy of *Galathea squamifera* Leach (Decapoda), with some histological detail of most structures described. The larvae have been omitted, as they are dealt with adequately by other authors. Some notes on reproduction and growth rate have been included. Attention has been paid to comparisons of the anatomy of the main organ systems of *Galathea* with that of corresponding systems, both in other members of the Anomura and also in other Decapoda. This has led to a tentative suggestion on the possible origin of the Anomura from a thalassinid ancestor and on their relationship with the rest of the Decapoda. R.B.P.

FACILITATION IN SEA ANEMONES. I. THE ACTION OF DRUGS. II. TESTS ON EXTRACTS

By **D. M. Ross**

J. Exp. Biol., Vol. 22, 1945, *pp.* 21–36

About twenty-five drugs, mostly those which act on vertebrate neuromuscular systems, were tested on *Calliactis parasitica* in an attempt to throw light on the mechanism of neuromuscular facilitation described by Pantin. No direct contractions of the musculature were elicited, but a few of the drugs which act at adrenergic junctions, tyramine, tryptamine and 933 F, caused responses to single stimuli. This might be described as a sensitizing or 'facilitating' effect, since two stimuli are required to initiate contractions of the sphincter in untreated animals. Adrenaline itself was inactive in this respect, but other drugs belonging to this group, cocaine and ergotoxine, had potentiating and inhibitory effects respectively which closely resembled their action at sympathetic junctions in vertebrates. Acetylcholine and allied drugs had no significant effects on facilitation. Extracts of *Calliactis parasitica* and *Metridium senile* also caused responses to single stimuli, but these differed from the tyramine effect in certain respects and it is unlikely that the two effects occur in exactly the same way. The results are consistent with the view that there are two processes taking part in neuromuscular transmission in these animals and that at least one of these processes involves sensitization of the muscle or the junctions by a chemical substance liberated by each nerve impulse.

D.M.R.

The Pallial Organs in the Aspidobranch Gastropoda and their Evolution throughout the Mollusca

By **C. M. Yonge**

Phil. Trans. Roy. Soc., B, Vol. 232, 1947, *pp.* 443–518

The probable conditions in the mantle cavity of the primitive Mollusca are described in the light of work on all available aspidobranch Gastropoda. Ctenidia, hypobranchial glands and osphradia are shown to constitute a functional unit. The nature of the primitive ctenidium precluded life on soft substrata; this was made possible in the Gastropoda by the evolution of the pectinibranch ctenidium. The effects of (1) torsion and (2) asymmetrical coiling of the shell on the pallial organs in the Gastropoda are discussed. These include important effects on the reproductive as well as on the respiratory system. In the aspidobranchs four conditions are shown to have resulted from the initial asymmetrical coiling of the shell. These include the acquisition of a secondarily symmetrical limpet form which has been independently achieved four times by them as well as several other times by higher Gastropoda. In the Patellacea a functional series, *Patelloida-Lottia-Patina-Patella*, is described. The evolution throughout the molluscan classes of the various types of ctenidia is described. Attachment may be either by the efferent or afferent side of the axis, but the arrangement of the afferent and efferent blood vessels remains constant throughout. It is the further elaboration of frontal and abfrontal cilia, originally concerned with cleansing the ctendia, that is responsible for the evolution of the food-collecting ctenidia of the majority of the Lamellibranchia. Further evidence is provided in support of the view that the osphradia are tactile organs concerned with estimating the amount of sediment carried in with the inhalant current. C.M.Y.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1947–48

The Council and Officers

Four ordinary meetings of the Council were held during the year, three in the rooms of the Royal Society and one at Plymouth. At these the average attendance was sixteen. The Association is indebted to the Council of the Royal Society for the use of its rooms.

The Council has to record with great regret the death of the Earl of Stradbroke, K.C.M.G., C.B., C.V.O., who was a Vice-President of the Association from 1910.

The Plymouth Laboratory

The rebuilding of the east wing of the main building as laboratory accommodation has proceeded slowly but steadily. The major construction is now completed, and the work on the interior is proceeding.

Aquarium

The tanks in the aquarium have been kept well stocked and they have attracted a considerably larger public than in pre-war days. During the year 83,237 tickets of admission have been sold, the receipts from which amount to £1770.

The sea water appears to be in better condition than before the war, large numbers of the tunicates, *Ciona* and *Molgula*, and the sponge *Sycon* growing naturally in the tanks and reservoirs. Objects of special interest displayed during the year have been sea horses from Arcachon and a turtle which came ashore in November 1947 at Newlyn.

A new edition of the abridged *Aquarium Guide* by Mrs E. W. Sexton and Mr D. P. Wilson has been printed, and it includes some of Mr Wilson's own photographs. Over 6800 copies have already been sold.

Research ships

The research vessel *Sabella* has been in commission all the year and is in excellent condition. During a survey in the summer considerable galvanic corrosion was found in the neighbourhood of the rudder caused by the presence of the copper sheathing on the hull. It is hoped that the special treatment given will keep this in check.

The motor boat *Gammarus* has run continuously throughout the year, and the motors and hull are in first-class condition.

Approval has been obtained from the Development Commissioners for the purchase by the Association of an additional research vessel intermediate in size between the *Sabella* and the *Gammarus*. A half-completed Admiralty 61½ ft. motor fishing vessel fitted with a 105 h.p. Lister engine has been purchased. The vessel is being completed by the Sittingbourne Shipbuilding Company in whose yard she was built, and Mr G. A. Steven has given much time to the planning of this vessel and superintending her completion. It is hoped that, with an extra research vessel available, the *Sabella* will be enabled to spend more time on scientific cruises and exploration of grounds farther afield. During the year the off-survey and sale of the *Salpa* have been effected. The Ministry of Transport lump-sum compensation and purchase monies together amount to about £4500.

Government Surplus and other Equipment

The Association has continued to take advantage of the opportunities afforded for obtaining apparatus from surplus Government stores, and use has especially been made of facilities given locally by the Devonport Dockyard. The Association is especially indebted to Mr J. L. Parkinson of the Biophysics Research Unit, University College, London, for assistance and advice regarding surplus apparatus. The thanks of the Association are also due to the Admiralty for the loan of a depth-recording instrument for use with plankton nets, and also of an outboard echo-sounding installation for use on the *Sabella*. The latter loan arose out of a recommendation by Mr M. N. Hill, who has been using it in submarine seismic investigations undertaken from the Plymouth laboratory in collaboration with Mr P. L. Willmore of the Department of Geodesy and Geophysics, Cambridge.

A Geiger-Müller counter has been lent to the Association by the Ministry of Supply for use at the Plymouth laboratory.

The Staff

Dr Mary W. Parke has been appointed to the staff as Botanist; she took up her appointment on 1 April 1947.

The recommendations submitted by the Development Commissioners for the assimilation of the staff to the grades of the Scientific Civil Service have now been approved by H.M. Treasury. The new grading is as follows: Senior Principal Scientific Officers: Mr E. Ford, Dr W. R. G. Atkins, F.R.S., and Dr H. W. Harvey, F.R.S.; Principal Scientific Officers: Mr G. A. Steven, Mr D. P. Wilson and Dr L. H. N. Cooper; Senior Scientific Officers: Mr G. M. Spooner, Dr Mary W. Parke and Mr P. G. Corbin; Scientific Officer: Mr H. G. Vevers; Experimental Officers: Mr S. M. Nunn and Mr F. J. Warren.

Dr W. R. G. Atkins, Mr G. M. Spooner and Mr F. J. Warren spent a few days in December 1947 at the Atomic Energy Research Establishment at Harwell, gaining experience in the use of the Geiger-Müller counter.

Mr G. A. Steven attended the thirty-fifth meeting of the International Council for the Exploration of the Sea held at Copenhagen in October 1947.

Mr D. P. Wilson has been awarded the Rodman Medal of the Royal Photographic Society for photomicrographs of the development of *Ophiothrix*.

Occupation of Tables

The following seventy-three workers have occupied tables at the Plymouth laboratory during the year:

Dr N. Ambache, London (Nerve net of Scyphomedusae).
Miss E. J. Batham, Cambridge (Nerve net of *Metridium*).
Dr Anna M. Bidder, Cambridge (Digestive system of *Loligo*).
Dr C. Francis-Boeuf, Paris (Chemistry of iron and chemical hydrography).
L. R. Brightwell (Aquarium).
Miss E. M. Brown, London (Parasitic and saprozoic Protozoa).
Dr M. Burton, British Museum (Nat. Hist.) (Sponges).
K. H. Chapman, Manchester (Morphology and bionomics of *Machilis*).
K. Chidambaram, Cullercoats (Fisheries).
J. S. Colman, Sheffield (Shore ecology).
Dr S. M. Das, Cullercoats (Excretion in Tunicates; *Folliculina*).
P. R. Day, London (Marine Algae).
Dr G. E. R. Deacon, Teddington (Library).
P. S. B. Digby (Planktonic Copepods).
E. B. Edney, Birmingham (General zoology).
Dr M. A. Ellison, Sherborne (Photo-electric cells).
D. Etherington, London (Sporozoan parasite in *Phascolosoma*).
Miss G. C. Evans, Leicester (Behaviour of *Lepidochiton*).
J. E. Forrest, London (Digestion in Dorids).
Dr V. Fretter, London (Molluscs).
D. J. Fryer, London (Elasmobranch and teleost nerve fibres).
K. D. Gibson, Cambridge (Plankton).
Dr Isabella Gordon, British Museum (Decapod Crustacea).
Miss U. M. Grigg, Cambridge (Biology of Trochids).
N. Guppy, Cambridge (Library).
Dr T. J. Hart, Discovery Investigations (Ice diatoms; hake).
P. H. T. Hartley, Oxford (Blennies).
M. R. Haywood, Leicester (Mechanism of the heart-beat of Tunicates).
H. F. P. Herdman, Discovery Investigations (Oceanographical Apparatus).
M. N. Hill, Cambridge (Seismic prospecting of sea-bed).
A. L. Hodgkin, Cambridge (Nerve fibre of *Loligo*).
F. S. J. Hollick, Cambridge (General zoology).
N. A. Holme, Cambridge (Bottom fauna).
Dr G. F. Humphrey, Cambridge (Inhibition of respiration of flagellates).
A. H. Al-Hussaini, Alexandria (Alimentary canal of fish).
J. D. Jones, Colonial Office (Physics and chemistry of sea water).
Dr C. B. Jörgensen, Copenhagen (Water transport through animals).
Dr B. Katz, London (Nerve fibre of *Loligo*).
K. L. Kermack, London (Spatangoids).
F. G. W. Knowles, Marlborough (Pigment movement in Crustaceans).

Dr T. Levring, Göteborg (Plymouth marine flora).
Dr O. C. J. Lippold, London (Nerve net of Scyphomedusae).
Dr O. Lowenstein, Glasgow (Electro-physiology of the elasmobranch labyrinth).
Dr A. G. Lowndes (Density of aquatic organisms).
Dr A. Marcotte, Quebec (General Marine Biology).
M. D. Menon, Madras (Fisheries).
H. P. Moon, Leicester (Mechanism of the heart-beat of Tunicates).
Miss V. Moyle, Cambridge (Excretion in Amphipods).
A. R. Natesa Iyer, Manchester (Library).
Prof. J. H. Orton, Liverpool (*Patella*).
Dr C. F. A. Pantin, Cambridge (Nerve net of *Metridium*).
P. E. Purves, British Museum (Methods of Echinoderm preservation).
Q. H. Qureshi, London (Fish embryology).
Dr J. Read, London (Action of radon on *Echinus* eggs).
Dr W. J. Rees, British Museum (Mollusca).
J. D. M. Roberts, Edinburgh (Electro-physiology of the elasmobranch labyrinth).
Miss H. G. Q. Rowett, Plymouth (Library).
Miss M. Sharman, London (Biology of Veneridae).
Prof. C. J. Shen, Peiping (Colour changes in *Crangon* larvae).
Miss J. Singer, Cambridge (Regeneration in Hydroids).
Dr R. Staempfli, Berne (Nerve fibre of *Loligo*).
Miss F. A. Stanbury, Plymouth (Library).
R. Subrahmanyan, Liverpool (Library).
Miss M. Taylor, London (Schizogregarine parasite in *Phascolosoma*).
P. K. Thomas, London (Elasmobranch and teleost nerve fibres).
Y. R. Tripathi, Allahabad University (Parasites of fishes).
D. W. Tucker, Liverpool (*Patella*).
Miss Vidya Vati, Lucknow University (Fish embryology).
R. Venkataraman, Madras (General).
Dr E. J. Wilkie, Portsmouth (Antifouling compositions).
P. L. Willmore, Cambridge (Seismic prospecting of sea-bed).
Dr and Mrs Claude E. ZoBell, Scripps Institution, La Jolla (General).

Again this year a very large number of visitors have taken the opportunity of spending a day or two in Plymouth to see the work of the laboratory. Among these, the following have come from overseas: Prof. A. B. L. Beznak, Tihany; Dr A. F. Bliss, Boston; Prof. Maurice Fontaine, Paris; D. T. C. Gillespie, Australia; Dr Sven Hörstadius, Uppsala; Dr and Mrs I. Bohus Jensen, Copenhagen; Prof. C. C. John, Travancore; K. F. King, Fisheries Officer, Palestine; Dr A. Lindenberg, Paris; Dr R. Overman, Tennessee; Prof. Carlos Peaz Perez, Colombia; Dr A. Punt, Utrecht; Prof. P. Sawaya, San Paulo; R. J. Swaby, New South Wales; Dr K. F. Vaas, Buitenzorg, Java; Prof. F. R. Zuniga, Chile.

The usual Easter Vacation Courses were conducted by Mr D. P. Wilson and Mr G. A. Steven, and were attended by forty students from the following Universities and University Colleges: Oxford, Cambridge, London, Edinburgh, Glasgow, Liverpool, Birmingham, Bristol, Leicester, Cardiff, Sheffield, Exeter and Newcastle.

Also during the Easter Vacation Mr R. Bassindale brought nineteen students from Bristol University. This was followed by a class of twenty-six boys brought by six masters from the following schools: Bradfield College, Christ's Hospital, Clayesmore School, Harrow and Wellington College.

During August a Refresher Course for biology teachers was conducted by Dr J. E. Smith and Dr G. E. Newell, at which the attendance, which included some students, was twenty-three.

A joint meeting of the Challenger Society and representatives from Marine Laboratories, under the Development Commissioners' Scheme, was held at the Plymouth laboratory on 10 and 11 July 1947. Members of the staff provided the papers and demonstrations for the meeting which was attended by some 90 persons.

Scientific Work of the Plymouth Laboratory Staff

Physics and Chemistry of Sea Water

Dr W. R. G. Atkins has been occupied in preparing for publication work done before or during the war, and in overhauling of general apparatus and electrical equipment. The entire assembly for photoelectric measurements has required careful examination; in particular he and Dr H. H. Poole are following up the ageing of rectifier cells and the suitability of newer types for use at sea. Some submarine measurements have also been made, partly in connexion with preliminary work on under-water visibility, partly for a comparison of two quite distinct physical measurements, the vertical extinction coefficient and the extinction coefficient as determined in a narrow tube. The latter is being measured by Dr Cooper with the Pulfrich photometer. Work on the preservation of nets has been held up pending the restoration of access to the Pier Cellars basin, but nets in use here and those sold to other institutions are treated with a copper soap mixture.

Observations now extending over a period of seventeen years have continued to show a well-marked relation between the quantity of plankton and young fish in the water off Plymouth and the quantity of phosphate in the water when at a maximum at the beginning of each year. Consequent upon this Dr H. W. Harvey has been engaged upon an investigation of the cycle of phosphorus in the sea, with the aim of finding whether the total phosphate and organic phosphorus compounds in the water at other times of the year than winter is related to the potential fertility of the water mass. Data are being obtained in collaboration with Mr P. G. Corbin's survey of plankton in the English Channel and in collaboration with Mr R. S. Wimpenny, of the Ministry of Agriculture and Fisheries' Laboratory at Lowestoft, in the North Sea. These data do not yet extend over a sufficient period of time. Some experiments have also been made on the rate of phosphate excretion by two species of animals filter-feeding on varied concentrations of phytoplankton.

The initial step in the investigation was to find fairly rapid methods of estimating the dissolved organic phosphorus in sea water and of estimating phosphate in solution with maximum accuracy. A suitable photoelectric instrument has been developed, a critical examination of the molybdenum-blue reaction in sea water has been made, and particulars of methods of estimation are being published in Vol. XXVII, No. 2 of the *Journal*. Means of storing water samples while in transit to the laboratory have also received attention in order to preclude adsorption of organic phosphorus compounds on the glass and to stop change in the phosphate content of the water.

During the course of this examination of methods of analysis it was found that the sea off Plymouth contained an unexpectedly low concentration of arsenic. This may prove of interest in view of recent work by Swedish botanists who find that this element is necessary for, or greatly stimulates, algal growth.

A method of estimating manganese in sea water is also under investigation. It has been found that several species of flagellates would not make continued growth in water from this area without the addition of 1 mg. or less manganese per cubic metre. Crude preliminary estimations are indicating that the water contains only a fraction of 1 mg. of manganese per cubic metre in this area.

The survey of quantitative physical, chemical and biological data from the English Channel started by Dr L. H. N. Cooper last year has been continued. In the earlier years of the nutrient salt investigations at Plymouth the whole of the western English Channel was usually occupied by a uniform body of water of which the station E1, 10 miles south-west of the Eddystone, was typical. In 1930, in the neighbourhood of Plymouth, phosphate-rich 'elegans' or 'western' water was replaced by 'setosa' or 'Channel' water. It had become doubtful whether station E1 was any longer so widely representative. In January 1947 R.V. *Sabella* was based on the port of Newlyn where a temporary chemical laboratory was set up. In spite of bad weather Mr Corbin worked twenty-three stations. In three areas the water was markedly different from that at E1. Two were phosphate-richer, one phosphate-poorer. High salinity and temperature, combined with the biological indicators, showed this latter to be 'south-western' water which had recently entered the Channel. These results provide the first indication of the phosphate content of 'south-western' water.

As a secondary theme, Dr Cooper studied the distribution of iron. These results are being published in Vol. XXVII, No. 2 of the *Journal*, and they indicate that iron is present in the sea as particles distributed at random.

In another paper landings of spurdog and of rays and skates have been compared with the yearly fluctuations of stocks of phosphate. Close parallels have been found.

The study of tidal kinetic energy has been continued. Many planktonic species able to live in the western English Channel cannot penetrate into the eastern half. The barrier seems to be—or to be associated with—the notable increase in kinetic energy of the tides in about 2° W. Publication has been delayed since the Admiralty have placed additional very useful tidal measurements at his disposal. These have still to be worked up.

Understanding of the present-day hydrology of the Channel and adjacent waters requires an intimate knowledge of the bottom topography. When studying banks and currents, it would be of much value to know which is caused by which. Sea-levels, temperatures and possibly salinities have changed much during the Pleistocene period, providing a series of differing environments for plants and animals. These changes ought to be considered in any study of the relationship of living organisms and their chemical and physical environment. The chaetognath *Sagitta setosa* provides an example. To-day this has its centre of distribution in the waters around the British Isles and North Sea, and it does not occur on the western side of the Atlantic. During the maximum withdrawal of the sea the area of its present habitat was mostly dry land, much of it heavily glaciated. To explain its present distribution, a knowledge of its evolution and whereabouts during the Ice Ages would seem essential.

Plankton

Mr F. S. Russell has resumed his work on the monograph of British medusae which was nearly completed before the war. He has brought it up to date as regards results published during the war by other authors on species which occur in the British fauna.

The observations which have been made for many years on the abundance of young fish and other plankton animals caught in weekly half-hour hauls with the 2 m. stramin ring are now being carried on by Mr P. G. Corbin. The results of this year's collections have been similar to those of last year, with *Sagitta setosa* dominant, but at no time numerous. *Muggiaea atlantica* appeared in considerable numbers in the late summer, but no *M. kochi* were present. The scarcity of young fish has continued.

Plankton collections taken with the 2 m. ring-trawl on a cruise in December 1946, and on three cruises in January 1947, all in the western Channel mouth area, are also being examined by Mr Corbin. Four cruises were originally planned for January, but the full programme was not carried out owing to bad weather. Conditions in January were severe, and the fact that it was possible to complete three cruises is in large measure due to the special weather forecasts which were provided twice daily for a particular sea area by the R.A.F. Meteorological Station, Mount Batten.

Mr Corbin is continuing work on the young fish of the 1937–9 mackerel investigation cruises. Some seventy-five species have been recorded, including a number of interesting oceanic species taken at stations near the edge of the Continental Shelf. The young stages of *Ammodytes* from these cruises are separable into four types, each of which can be distinguished by marked pigmentation differences. Types I and IV are respectively *A. lanceolatus* and

A. tobianus, type II appears to be *A. marinus*, while type III, although not yet identified, is not attributable to *A. cicerellus*, the young stages of which were described by Louis Fage from the Mediterranean. Adult *A. cicerellus* are, however, now known to occur in the Plymouth area, on three separate occasions this year single specimens being caught by R.V. *Sabella*. In the above researches Mr Corbin has been assisted by an Indian State Scholar, Miss Vidya Vati.

During the year Mr P. S. B. Digby has been working on a Development Commission Grant studying life histories of the smaller planktonic copepods. The work is based on weekly collections made at the International station L 4, 5 miles from Plymouth breakwater, with the Harvey measuring net, the Clarke and Bumpus plankton sampler, and townets. Cruises have been made in January, June and July to other parts of the Channel to give information on whether the breeding periods are advanced or retarded elsewhere.

The species investigated have been *Paracalanus parvus*, *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia clausi and Oithona similis*. Less complete data have been obtained for *O. nana* and *Centropages typicus*, and for the cyclopoids *Corycaeus* and *Oncaea*. The collections from August until October and most of the cruise samples are still to be worked up.

The winter plankton of early 1947 consisted of *Paracalanus*, *Pseudocalanus* and *Oithona* in roughly equal numbers, the only nauplii present in quantity being those of *Pseudocalanus*. Similar conditions prevailed on the south side of the Channel and in the area to the west of the Scillies, apart from the addition of late stages of *Metridia* and *Calanus* in the latter. By the end of February small numbers of *Acartia* and *Temora* had appeared and a brood of nauplii of the five main species occurred (with the possible exception of *Acartia*, found in very small numbers at this time of the year). A great increase in the number of nauplii of all species appeared in May and June, *Pseudocalanus* being first in May, *Paracalanus*, *Acartia* and *Temora* in May and June, and *Oithona* in June and July. The nauplii of all species were present continuously from February, and it is not yet clear whether in general there is a single long development period of 2½–3½ months from February to May or June, or whether there are two shorter periods, from February to May and from May to June or July, of about 2½ months and 1 month or 6 weeks respectively. If this latter is the case, the development times are closely comparable to those found by Fish in the Gulf of Maine, and the usual large spring increase of smaller copepods is due to the combined second and third generations of the year. This is expected to be clarified by further work on the samples.

Mr D. P. Wilson's investigations into the occurrence of the Portuguese Man-of-War (*Physalia physalis*), in the south-western area of England and Wales during the summer and autumn of 1945, have been completed and published in Vol. XXVII, No. 1 of the *Journal*. He shows, from a consideration of meteorological data for the period involved, that winds more than water currents move the swarms towards the British Isles and are mainly responsible for determining on what parts of the coastline they shall be stranded. It has not been possible to determine precisely the place of origin of the swarms, but the available evidence suggests that they are more likely to come to us from a region in mid-Atlantic west of the Azores than from the area between the Canaries and Gibraltar. The literature of the past hundred years has been searched for records of previous visitations to the Atlantic coasts of Europe, and these reveal that strandings in abundance may be expected to occur three or four times a century, with visitations in small numbers every several years. Some previously unpublished records for 1912, 1913, 1934 and 1935 were discovered in the laboratory, and these are listed and discussed in the paper.

Cultures of marine planktonic diatoms and flagellates have been maintained in the Plymouth laboratory by Dr Mary Parke. Much culture material has been used by research workers in the laboratory and subcultures have been sent to Norway, Holland, France and many institutions in Britain for research purposes.

Fauna and Flora of the Sea Floor

During the breeding season of the polychaete worm *Ophelia bicornis*, many more experiments were made by Mr D. P. Wilson in an endeavour to determine the nature of the stimulus initiating metamorphosis of the larva. The data so accumulated have still to be examined critically, but it would appear that the main factor responsible is the physical size and shape of the sand particles, or, put another way, the sizes and shapes of the interstices between the grains. Sands much finer or coarser than that of the natural adult habitat or sands of angular instead of rounded grains, are definitely less attractive to the larvae than is sand from the natural habitat. Unsuitable sands delay metamorphosis and the larvae may die without metamorphosing at all. So far no indication has been obtained that sand from the adult habitat contains any slightly soluble substance able to initiate metamorphosis in the absence of suitable sand particles, but it is intended to make further experiments on this and other aspects next breeding season. Some experiments were made to test the ability of the larvae to distinguish between sands of various sorts contained in separate compartments of the same dish. While the results were not entirely satisfactory they did yield some positive evidence of ability to choose aright, but the absence in the experimental dishes of strongly flowing water, such as would be present in nature, seems to have affected adversely these particular tests.

The paper by Mr G. M. Spooner dealing with the taxonomic side of estuarine *Gammarus* species was published in Vol. XXVII, No. 1 of the *Journal*, and an interesting development immediately arising out of it has been followed up. The necessity for splitting *G. zaddachi* (as described in last year's Report) had been independently recognized by Dr Segerstråle of Helsingfors, with whom there have been some useful exchanges of material and opinions. Agreement has been reached on the status of the northern marine populations hitherto assigned to *G. locusta*. These have clearly to be transferred from that species, from which they differ in many important respects, to be included under *G. zaddachi*. A third subspecies, *G. z. oceanicus*, is erected by Segerstråle to include them.

G. z. oceanicus is told mainly by the form and setation of the first antenna which is intermediate between typical *zaddachi* and *locusta* and, apparently, by the lack of pigment bands on the hinder part of the body, a feature which disappears in preserved material. The northern cold-water populations are distinguished readily enough by their larger size, but at the southern limit of their range they are much closer in appearance to *G. z. salinus*. It occurs abundantly along the coast of Norway, and in the Baltic Sea in much lower salinities.

G. zaddachi is thus a widely spread arctic-boreal species which ranges into temperate waters where it becomes an exclusively brackish water, or even fresh-water, animal.

In Britain *G. z. oceanicus* has been recognized in material from the northern half of Scotland. It occurs in the Tay estuary at the level normally inhabited by *G. z. salinus*. In some parts of Scotland there is presumably an overlapping of its range with that of *salinus* (as occurs widely in the Baltic), but this matter requires investigation. It has also yet to be shown that *oceanicus* and *salinus* are intersterile, as *salinus* and typical *zaddachi* have been shown to be.

Over most of the British Isles, however, only *G. z. zaddachi* and *G. z. salinus* appear to be present. Their occurrence in population samples from estuaries and other brackish waters is the main subject of Part II of the material which is in preparation for publication.

With *G. locusta* (*sens. strict.*) these two provide useful 'indicators' for zoning habitats of estuaries. Passing from the sea to the upper limit of tidal influence there are six zones. In (1) at the seaward end the population consists entirely of *G. locusta*; in (2) of a mixture of *G. locusta* and *zaddachi salinus*; in (3) in the middle reaches (where the fluctuation of salinity is greatest and where the fauna and flora is least varied) of *G. z. salinus* only; in (4) of a mixture of *G. z. salinus* and *G. z. zaddachi*; in (5) of *G. z. zaddachi* only, living normally; and in (6) *G. z. zaddachi* present but not breeding and *G. pulex* often present. Changes in the population follow the major seasonal fluctations, such as occur between summer and winter. The distribution of other members of the fauna, such as the crustaceans *Marinogammarus marinus* and *Cyathura carinata*, and the molluscs *Cardium edule*, *Scrobicularia plana*, *Hydrobia ulvae* and *H. jenkinsi*, and *Littorina* spp., etc., can be related to these zones.

Mrs E. W. Sexton, with the kind collaboration of Mr D. M. Reid, has been preparing the results of the investigation of the diversity of form in the amphipod species *Jassa falcata* (Montagu). It is hoped the work will soon be ready for publication.

Mr H. G. Vevers has continued his studies on the breeding biology of the common starfish *Asterias rubens*, in the waters off Plymouth. The main work has been carried out on population samples of this species taken throughout the year from two different areas to the south of Plymouth. The populations in these areas were very distinct in size composition, those from the inshore area being medium-sized (as defined by size ranges and means), while those on the offshore grounds (to the south and south-west of Eddystone) were more numerous and consisted of essentially large starfishes, reaching in some cases over 30 cm. in radius. Examination of the gonads showed a further marked difference between the two populations. In the inshore area less than 30% of the females reached full maturity between the beginning of April and the middle of June, whereas in the offshore population over 60% of the females reached this stage and showed ripe eggs between mid-March and mid-May with a peak in the middle of April. Townet catches taken throughout the season contained bipinnaria larvae between the middle of April and the end of May.

The bottom temperatures in the two areas do not differ greatly and there does not appear to be any direct correlation between temperature and the differences in ovarian maturity observed in the two areas. The high value for ripe ovaries in the offshore population is tentatively regarded as a direct reflexion of the richer food resources (especially the shoals of *Chlamys* (*Pecten*) *opercularis*) available in this area as compared with those available farther inshore. The successful maturing of the offshore population is not dependent upon the large size of the individuals, but both these attributes are considered to be the direct result of the rich food supply. In further support of this view it was found that in a third area (closer inshore) where there was a rich stock of food lamellibranchs, the starfishes were smaller (half the size) than those of the 'inshore' population, and yet they were in full breeding condition at the end of May. From laboratory observations on rate of growth it appears that these small but breeding starfishes could easily have reached this size in one year from metamorphosis.

The parasitic ciliate, *Orchitophrya stellarum* Cépède, was found in the gonads of up to 20% of the 'offshore' males during the breeding season. This parasite was first recorded as very rare on the north coast of France and has since been recorded in two related species of *Asterias* in North America; it has not previously been recorded at Plymouth. It causes parasitic castration in the testes where it is present, and its distribution throughout the population has been studied in some detail.

Further research on bottom animals has been started by two students at the laboratory on D.S.I.R. Maintenance Grants, Miss U. M. Grigg and Mr N. A. Holme, who began their work on 1 October. Miss Grigg is studying the ecology of the four species of Trochid molluscs occurring on our shores, and Mr Holme is devoting his attention to problems connected with the bottom fauna.

Dr Mary Parke has continued working up the results of the investigations on seaweeds, and the first paper dealing with *Laminaria saccharina* (L.) Lamour. is nearly completed.

Further points of interest have emerged from the detailed study of the data relating to *L. saccharina* which were amassed during the practical side of the work. It has been shown that the variation that can be found in this species on the British coast can be related to the variation in the rate of growth of the plants with changes in age, season, habitat and geographical position. Not only can growth forms be classed as varieties of the species, some of the forms obtained during the work agree even with descriptions of distinct species.

The differential growth rate in length at successive levels up the frond of plants of *L. saccharina* has been worked out. The results show that the primary or basal growth never drops below 70% of the total frond growth in length. On the Argyll coast primary growth shows the highest percentage of the total increase from October to April with the peak from December to February. In the frond tissue above the base the highest percentage increase (secondary growth) is from August to October, when the lowest percentage of primary growth is recorded. It has been found that in plants growing on the Devon coast the peaks of primary and secondary growth occur one month earlier than on the Argyll coast.

The figures for the width of the frond of plants at different ages, in different habitats and geographical positions, show that the width of the frond tissue produced is in direct relation to the rate of growth in length of the frond. It has been shown that with the variation in the rate of growth in frond length and width throughout a yearly cycle a change takes place in the shape of the base of the frond, so that the rapidity or the slowness of the frond growth at any time can be assessed roughly from the shape of the frond base.

The regenerative powers of different-aged plants of this species have been investigated. It has been found that when the whole frond is removed from a plant no regeneration occurs, and that when a frond is cut or torn off near the base complete regeneration of the frond occurs only in plants up to the age of one year.

Dr Parke is building up a collection of preserved specimens of marine algae at the Plymouth laboratory, and she has made a number of additions to the recorded species. She has also been engaged in compiling a summary and bibliography of all work done on marine algae in Great Britain and Ireland during the war for publication in the *Revue Algologique*.

Fishes and Fisheries

In last year's report Mr E. Ford briefly described a method of defining the spatial form of the neurocranium in species of gadoid fishes by means of a geometric network passing through the natural centres of the individual skull bones. During the present year, the work has been extended to cover some twenty different species, in order to determine the nature and extent of variation between them. Comparisons have also been made between skulls of cod caught in widely separated localities, to test the possibility that skull-form in the one species is subject to geographical variation. A necessary development of the technique was to study the form and disposition of the individual skull-bones. For although the geometric network depicts the orientation of the bones by means of their centres, it does not take into account their varying size and shape, and the degree of overlap between them, which is often quite considerable. To obtain information of this kind it is necessary to examine the interior of the skull as well as the exterior, and to disarticulate the skull, bone by bone.

Mr Ford has collaborated with Miss Vidya Vati in a study of the keeled scales in young herring, sprat and pilchard. The keeled scales lie in a median row along the ventral edge of the body from the throat backwards to the anus, and normally they are in meristic register with the myocommata, ribs and vertebrae. In the region of the pelvic fins, however, this agreement is liable to break down. Until further information is available concerning the extent to which this breakdown occurs, statistical counts of keeled scales in population studies will be subject to error of unknown magnitude. Comparison between the keeled scales of young herrings from Plymouth and those from the Clyde revealed distinctive differences in form—so much so that a mixed sample of the two could be resorted by mere inspection of the keeled scales in each individual.

Mr G. A. Steven has continued to work up the results of his mackerel investigations in the south-western area. A paper has been completed and will shortly be published on 'Mackerel Migrations in the English Channel and Celtic Sea'. In the light of this work it is believed that the hitherto imperfectly understood migratory habits of the *Scomber scombrus* on both sides of the North Atlantic will be found to fit into one coherent and relatively simple picture. There is each year a demersal period, a pelagic migratory period during which spawning takes place, and a brief transition period in which the fish return from the surface waters to winter quarters on the sea floor.

There is a very long spawning season extending from March till July with maximum intensity in April. This is due to the fact that the mackerel of the area do not all spawn at the same time. Another contributory factor is that in these fish the eggs mature in batches that are spawned in succession over an extended spawning period. Ripe, translucent eggs appear in the ovary distributed widely and irregularly amongst the still unripe, yellowish ova, giving rise to a peculiar speckled appearance that, for lack of a better term, has been called the 'plum pudding' stage. These ripe ova are dehisced into the lumen of the ovary which then, on superficial examination, shows no trace of ripe eggs. Unless opened up, such an ovary may well be, and often has been, described as 'unripe'. In the mackerel, in fact, a fully 'ripe' ovary is never present; the most that is ever found is an ovary containing small numbers of ripe eggs.

These observations are being worked up, but additional information is needed on some difficult points. Unfortunately, as there has been no spring mackerel fishery since the war, no samples of spawning fish have been obtainable. It is hoped that fishing will be renewed next spring so that further investigations can then be made.

The Library

The thanks of the Association are again due to numerous foreign Government Departments, and to Universities and other Institutions at home and abroad, for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the *Journal*. Thanks are also due to those who have sent books or reprints of their papers, which are much appreciated.

During the year the periodicals in the Library have been checked and listed for inclusion in the next edition of *The World List of Scientific Periodicals.*

Published Memoirs

Vol. XXVI, No. 4 of the *Journal* was published in June 1947, Vol. XXVII, No. 1 in November 1947, and Vol. XXVII, No. 2 is nearing completion.

The following papers, the outcome of work done at the laboratory, have been published elsewhere than in the *Journal* of the Association:

ATKINS, W. R. G., 1947. Disappearance of *Zostera marina*. *Nature*, Vol. 159, p. 477.

ATKINS, W. R. G., 1947. Size versus colour in air-sea rescue. *Nature*, Vol. 159, pp. 612–13.

ATKINS, W. R. G., 1947. Electrical conductivity of river, rain and snow water. *Nature*, Vol. 159, p. 674.

ATKINS, W. R. G. & ELLISON, M. A., 1947. Photoelectric measurements of the seasonal variations in daylight at Plymouth, from 1938 to March 1941, compared with the years 1930 to 1937. *Proc. Roy. Soc., London*, A, Vol. 191, pp. 467–84.

COOPER, L. H. N., 1947. Internal waves and upwelling of oceanic water from mid-depths on to a Continental Shelf. *Nature*, Vol. 159, pp. 579–80.

COOPER, L. H. N., 1947. Recent work of the Marine Biological Laboratory, Plymouth. *British Science News*, Vol. 1, pp. 8–10.

HART, T. JOHN, 1948. The distribution and biology of hake. *Biological Reviews*, Vol. 23, pp. 62–80.

HILL, M. N. & WILLMORE, P. L., 1947. Marine seismic prospecting. *Nature*, Vol. 159, pp. 707–8.

JEPPS, MARGARET W., 1947. Contribution to the study of the sponges. *Proc. Roy. Soc., London*, B, Vol. 134, pp. 408–17.

LEBOUR, MARIE V., 1947. The oyster. II. *School Science Review*, Vol. XXVIII, pp. 216–19.

NICOL, J. A. C. & YOUNG, J. Z., 1946. Giant nerve fibre of *Myxicola infundibulum* (Grube). *Nature*, Vol. 158, p. 167.

PIKE, RICHARD B., 1947. *L.M.B.C. Memoir*, XXXIV. *Galathea* (in part). Liverpool University Press. 178 pp.

REES, W. J., 1947. On the systematic position of the Hydroid genera *Hippolytus* Murbach, 1899, and *Dahlgrenella* Miles, 1937. *Ann. Mag. Nat. Hist.* (11), Vol. XIII, pp. 102–6.

RUSSELL, F. S., 1947. The Plymouth Laboratory of the Marine Biological Association of United Kingdom. *Proc. Roy. Soc., London*, B, Vol. 135, pp. 12–25.

SPOONER, G. M., 1947. Further extension of the range of *Crepidula fornicata* (L). *Journ. of Conchology*, Vol. 22, p. 243.

STEVEN, G. A., 1947. The British Raiidae. *Science Progress*, Vol. XXXV, pp. 220–36.

STEVEN, G. A., 1947. *Report on the Sea Fisheries of Sierra Leone.* (Freetown, 1945.) Crown Agents for the Colonies, Millbank, London, 1947. 66 pages.

STEVEN, G. A., 1948. The Plymouth Marine Biological Laboratory. *Discovery*, February 1948, pp. 43–9.

WILSON, D. P., 1947. *They Live in the Sea.* Collins: London. 128 pp.

YONGE, C. M. 1947. The pallial Organs in the Aspidobranch Gastropoda and their evolution throughout the Mollusca. *Phil. Trans. Roy. Soc., London*, B, Vol. 232, pp. 443–518.

Membership of the Association

The total number of members on 31 March 1948 was 458, being 46 more than on 31 March 1947; of these the number of life members was 69 and of annual members 389. The number of Associate members is now three, Dr H. Muir Evans having died during the year.

Finance

General Fund. The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

Private Income. The Council gratefully acknowledges the following generous grants for the year:

From the Fishmongers' Company (£500), the Royal Society (£50), British Association (£50), Physiological Society (£30), the Ray Lankester Fund (£20), the Cornwall Sea Fisheries Committee (£10); the Universities of Cambridge (£125, and £20 balance for 1946-7), London (£210), Oxford (£100, and £52. 10*s.* for 1946–7), Bristol (£50), Birmingham (£31. 10*s.*), Manchester (£10. 10*s.*), Leeds (£20), Nottingham (£10. 10*s.*), Leicester (£10. 10*s.*), Exeter (£10. 10*s.*), Southampton (£10. 10*s.*), Sheffield (£5) and the Imperial College of Science and Technology (£10).

President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1948–49:

President

Prof. James Gray, C.B.E., M.C., Sc.D., LL.D., F.R.S.

Vice-Presidents

The Earl of Iveagh, C.B., C.M.G.
Viscount Astor
Sir Nicholas E. Waterhouse, K.B.E.
Sir Sidney F. Harmer, K.B.E., Sc.D., F.R.S.
Col. Sir Edward T. Peel, K.B.E., D.S.O., M.C.
Prof. Walter Garstang, D.Sc.
The Rt. Hon. Tom Williams, M.P.
G. P. Bidder, Sc.D.
W. T. Calman, C.B., D.Sc., F.R.S.
Vice-Admiral Sir John A. Edgell, K.B.E., C.B., F.R.S.
Prof. A. V. Hill, C.H., O.B.E., Sc.D., F.R.S.
E. S. Russell, O.B.E., D.Sc.
Sir Edward J. Salisbury, Kt., C.B.E., Sec.R.S.
Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O.

COUNCIL

To retire in 1949

G. E. R. Deacon, D.Sc., F.R.S.
Prof. J. E. Harris, Ph.D.
N. A. Mackintosh, D.Sc.
Edward Hindle, Sc.D., F.R.S.
R. S. Wimpenny

To retire in 1950

H. Cary Gilson
C. F. Hickling, Sc.D.
Morley H. Neale
Prof. Lily Newton, Ph.D.
Prof. J. Z. Young, F.R.S.

To retire in 1951

Anna M. Bidder, Ph.D.
Prof. J. Rogers Brambell, D.Sc.
J. N. Carruthers, D.Sc.
O. D. Hunt
J. E. Smith, Ph.D.

Hon. Treasurer

Major E. G. Christie-Miller, 38 Hyde Park Street, London, W. 2

Secretary

F. S. Russell, D.S.C., D.F.C., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. Bidder, Sc.D.
P. D. H. Dunn, C.M.G., O.B.E. (Ministry of Agriculture and Fisheries)
The Worshipful Company of Fishmongers:
  The Prime Warden
  Major E. G. Christie-Miller
  Alfred R. Wagg
Prof. A. C. Hardy, D.Sc., F.R.S. (Oxford University)
C. F. A. Pantin, Sc.D., F.R.S. (Cambridge University)
Prof. H. Gordon Jackson, D.Sc. (British Association)
H. G. Maurice, C.B. (Zoological Society)
Prof. A. V. Hill, C.H., O.B.E., Sc.D., F.R.S. (Royal Society)

BALANCE SHEET 1947–48

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH 1948

	£	s.	d.	£	s.	d.	£	s.	d.
SUNDRY CREDITORS:									
Accrued Expenses				386	2	11			
Subscriptions received in advance				40	12	4			
Grant received in advance				125	0	0			
Admiralty—Hire of R.V. 'Sabella'				2530	0	0			
Equipment for R.V. 'Sula'				326	14	0	3408	9	3
AQUARIUM SINKING FUND:									
As at 31st March 1947				332	3	11			
Add: Donations for rebuilding Aquarium Tanks:									
Plymouth Corporation ...	100	0	0						
Aquarium Visitors ...	33	17	1	133	17	1			
				466	1	0			
Less: Transfer to Income and Expenditure Account				332	3	11	133	17	1
E. T. BROWNE—BEQUEST FUNDS:									
Building Fund, as at 31st March 1947	1265	1	9						
Add: Interest on Investment ...	38	7	3						
Profit on Redemption of Investment	13	14	0	1317	3	0			
Library Fund, as at 31st March 1947	1118	2	1						
Add: Interest on Investment ...	34	0	10						
Profit on Redemption of Investment	16	14	5	1168	17	4			
Special Apparatus Fund, as at 31st March 1947	2540	17	4						
Add: Interest on Investment ...	76	19	11						
Profit on Redemption of Investment	25	13	3	2643	10	6			
Scientific Publications Fund, as at 31st March 1947...	1905	12	8						
Add: Interest on Investment ...	57	15	0						
Profit on Redemption of Investment	19	8	0	1982	15	8	7112	6	6
'SALPA' DEPRECIATION FUND:									
As at 31st March 1947				6477	3	8			
Add: Amounts received from Ministry of Transport Compensation on De-requisitioning	3927	0	0						
Hire	33	10	0	3960	10	0			
Interest on Investments				238	15	6			

	£	s.	d.	£	s.	d.	£	s.	d.
BOATS AND EQUIPMENT, at valuation as estimated by the Director at 31st March 1941 plus Additions at Cost:									
S/S 'Salpa':									
As at 31st March 1947				2000	0	0			
Less: Net proceeds of sale ...	614	5	9						
Loss on sale	1385	14	3	2000	0	0			
Motor Boat 'Gammarus':...				200	0	0			
Nets, Gear and General Equipment:									
As at 31st March 1947	50	0	0						
Additions during the year ...	50	0	0	100	0	0	300	0	0
LABORATORY APPARATUS, ENGINES AND PUMPS, at valuation as estimated by the Director at 31st March 1941, plus additions at cost:									
As at 31st March 1947				4800	0	0			
Additions during the year				250	0	0	5050	0	0
LIBRARY, at valuation by Mr Ridgill Trout in January 1941, plus additions at cost:									
As at 31st March 1947				16100	0	0			
Additions during the year				250	0	0	16350	0	0
STOCKS ON HAND, as valued by the Director:									
Specimens				600	0	0			
Chemicals				250	0	0			
Journals				400	0	0	1250	0	0
SUNDRY DEBTORS:									
Sales of Specimens, etc.							673	10	1
PREPAYMENTS							247	3	4
RECOVERABLE EXPENDITURE:									
Research Fund—Miss N. G. Sproston:									
As at 31st March 1947				165	17	10			
Less: Grant received	165	11	8						
Transfer from Income and Expenditure Account ...		6	2	165	17	10			
Research Fund—P. S. B. Digby:									
Expenditure				581	6	4			
Less: Balance at 31st March 1947	7	13	10						
Grant received	533	16	8	541	10	6			
				39	15	10			
ON BUILDINGS RECONSTRUCTION:									
Expenditure:									
Rebuilding East Wing	5018	0	0						
Reconstruction of Main Building	1830	3	1						

	£ s. d.	£ s. d.	£ s. d.
Less: Maintenance to date of Sale	53 0 0		
Loss on Sale	1385 14 3		
Loss on Redemption of Investment	113 6 9		
Transfer to Vessels' Hire and Capital Expenditure Fund	9124 8 2		
		10676 9 2	— — —
VESSELS' HIRE AND CAPITAL EXPENDITURE FUND:			
Transfer from 'Salpa' Depreciation Fund ...		9124 8 2	
Add: Transfer from Income and Expenditure Account		850 0 0	
		9974 8 2	
Less: Hire of R.V. 'Sabella' for year to date	1380 0 0		
Modifications to R.V. 'Sabella'	800 0 0		
Equipment for R.V. 'Sula' ...	326 14 0		
		2506 14 0	
			7467 14 2
'GAMMARUS' REPLACEMENT FUND:			
As at 31st March 1947		564 15 4	
Add: Interest on Investment		16 12 0	
		581 7 4	
Less: Loss on Redemption of Investment ...		11 6 10	
			570 0 6
COMPOSITION FEES FUND:			
As at 31st March 1947		472 10 0	
Add: Fees Received		110 5 0	
		582 15 0	
Less: Loss on Redemption of Investment ...		9 6 10	
			573 8 2
BIOLOGICAL INVESTIGATIONS ON 'ALGAE' FUND:			
As at 31st March 1947			8 1 3
MACKEREL RESEARCH FUND:			
As at 31st March 1947		9 15 11	
Add: Transfer from Income and Expenditure Account		1 10 6	
		11 6 5	
Less: Repaid to Ministry of Agriculture and Fisheries ...	9 15 11		
Expenditure	1 10 6		
		11 6 5	— — —
SPECIAL SQUID TANK FUND:			
Grant received from Rockefeller Unit of Neurophysiology, Cambridge			70 0 0
CAPITAL RESERVE ACCOUNT:			
As at 31st March 1947			21688 8 2
SURPLUS ACCOUNT:			
As at 31st March 1947		3419 18 11	
Less: Excess of Expenditure over Income for the year		1537 9 8	
			1882 9 3
			£42,914 14 4

	£ s. d.	£ s. d.	£ s. d.	£ s. d.
Less: Balance on Building Reconstruction Fund at 31st March 1947	1372 3 5			
Grant received	5018 0 0			
		6390 3 5		
			457 19 8	
				497 15 6
GENERAL FUND INVESTMENT at Book Value £352. 2*s.* 3*d.* 2½% Treasury Stock ... ... (Market value at date £269. 7*s.* 0*d.*)				232 7 10
E. T. BROWNE—BEQUEST FUNDS INVESTMENT, at Cost: £7242. 14*s.* 10*d.* 3% British Transport Stock (Market value at date £7025. 0*s.* 0*d.*)				7112 6 6
VESSELS' HIRE AND CAPITAL EXPENDITURE FUND INVESTMENT, at cost: £4846. 11*s.* 9*d.* 2½% Treasury Stock ... ... (Market value at date £3717. 17*s.* 0*d.*)				4433 10 9
'GAMMARUS' REPLACEMENT FUND INVESTMENT, at cost: £580. 9*s.* 6*d.* 3% British Transport Stock ... (Market value at date £563. 1*s.* 0*d.*)				570 0 6
COMPOSITION FEES FUND INVESTMENTS, at cost:				
£18. 18*s.* 6*d.* 2½% Treasury Stock			15 15 0	
£567. 17*s.* 8*d.* 3% British Transport Stock ... (Market value at date £564. 19*s.* 0*d.*)			557 13 2	
				573 8 2
CASH AT BANK AND IN HAND:				
Coutts and Company			4919 0 10	
Lloyds Bank Limited			632 16 5	
Cash in Hand			72 14 5	
				5624 11 8
				£42,914 14 4

TO THE MEMBERS THE OF MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the Books of the Association and have obtained all the information and explanations we have required. Capital Expenditure on erection of Buildings on Land held on Lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs as at 31st March 1948 according to the best of our information and the explanations given to us and as shown by the books of the Association.

PRICE, WATERHOUSE & CO

Prudential Buildings, George Street, Plymouth.
19th May, 1948.

G. E. R. DEACON }
JOHN E. HARRIS } *Members of the Council.*

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1948

	£ s. d.	£ s. d.
To Salaries, including Association's Contributions to Superannuation and War Bonuses ...		14357 1 0
,, Laboratory and Boats' Crews' Wages, including National Insurance, Contributions to Superannuation Scheme, War Bonus and Employer's Liability Insurance		8941 17 4
,, Upkeep of Library		238 6 7
,, Scientific Publications, less Sales ...		994 15 2
,, Upkeep of Laboratories and Aquarium:		
Buildings and Machinery	411 12 1	
Electricity, Oil, Gas, Coal and Water ...	501 5 5	
Chemicals and Apparatus	837 5 9	
Fire Insurance, Tithe, Ground Rent and Rent of Store	114 6 5	
Travelling Expenses	344 2 7	
Stationery, Postages, Telephone, Carriage and Sundries...	725 17 10	
Specimens	292 7 1	
		3226 17 2
,, Expenditure in Connection with R.V. 'Sabella'		— — —
,, Maintenance and Hire of Boats:		
Petrol, Oil, Paraffin, etc.	232 1 1	
Maintenance and Repairs to Nets, Gear and Apparatus	1183 10 8	
Purchase of Materials for Nets, etc. for Resale	321 14 5	
Boat Hire, Collecting Expenses and Upkeep of Truck...	106 12 1	
Insurances	395 10 0	
Hire of R.V. 'Sabella'...	— — —	
		2239 8 3
,, Entertainment Expenses		24 6 6
,, Bank Charges		9 4 0
,, Transfer to Vessels' Hire and Capital Expenditure Fund		850 0 0
,, Transfer to Miss N. G. Sproston Research Fund, Irrecoverable balance		6 2
,, Transfer to Mackerel Research Fund, Irrecoverable balance		1 10 6
,, Transfer to Repairs and Renovations Fund		— — —
,, Transfer to Aquarium Sinking Fund ...		— — —
		£30,883 12 8

		£ s. d.	£ s. d.
By Grants:			
Ministry of Agriculture and Fisheries Grant from Development Fund		22600 0 0	
Fishmongers' Company		500 0 0	
British Association		50 0 0	
Royal Society		50 0 0	
Physiological Society		30 0 0	
Cornwall Sea Fisheries Committee		10 0 0	
			23240 0 0
,, Subscriptions (excluding Subscriptions received in advance)			404 6 7
,, Donations			— — —
,, Fees for Tests of Materials			86 8 6
,, Sales:			
Specimens		2221 14 7	
Photographs (*less* purchases)		27 6 2	
Fish		105 18 10	
Nets, Gear and Hydrographical Apparatus ...		399 17 9	
			2754 17 4
,, Table Rents (including Universities of Cambridge £145 (including £20 for 1946/47); London £210; Oxford £152. 10*s*. 0*d*. (including £52. 10*s*. 0*d*. for 1946/47); Bristol £50; Birmingham £31. 10*s*. 0*d*.; Leeds £20; Manchester £10. 10*s*. 0*d*.; Leicester £10. 10*s*. 0*d*.; Exeter £10. 10*s*. 0*d*.; Nottingham £10. 10*s*. 0*d*.; Southampton £10. 10*s*. 0*d*.; Imperial College £10; Sheffield £5; Trustees of Ray Lankester Fund £20 and Ministry of Works £104)			1029 18 8
,, Interest on Investments			20 4 8
,, Sale of Dr M. V. Lebour's Book			5 7 6
,, Sale of 'Plymouth Marine Fauna'			12 4 6
,, Aquarium:			
Admission Fees...		1770 7 3	
Sale of Guides		193 0 2	
Sale of Postcards		19 12 8	
Transfer from Sinking Fund		332 3 11	
		2315 4 0	
Less: Expenditure:			
Maintenance of Buildings	160 13 1		
Printing	214 8 2		
Food	75 8 0		
Wages	71 19 6		
		522 8 9	
			1792 15 3
,, Balance being Excess of Expenditure over Income for the year			1537 9 8
			£30,883 12 8

LIST OF GOVERNORS, FOUNDERS, MEMBERS, HONORARY AND ASSOCIATE MEMBERS

1948

GOVERNORS

The British Association for the Advancement of Science, *Burlington House, W.* 1
The University of Oxford
The University of Cambridge
The Worshipful Company of Clothworkers, 48 *Fenchurch Street, E.C.* 3
The Worshipful Company of Fishmongers, *London Bridge, E.C.* 4
  The Prime Warden. (**Council**, 1886→)
  Wagg, Alfred R., *The Hermitage, East Grinstead.* (**Council**, 1948→)
  Christie-Miller, Major E. G., 38 *Hyde Park Street, W.* 2. (**Hon. Treasurer**, 1941→)
The Zoological Society of London, *Regent's Park, N.W.* 8
The Royal Society, *Burlington House, Piccadilly, W.* 1
Ministry of Agriculture and Fisheries, *St Stephen's House, Victoria Embankment, S.W.* 1
Bayly, Robert (the late). (**Council**, 1896–1901)
Bayly, John (the late)
Browne, E. T. (the late). (**Council**, 1913–19; 1920–37)
Thomasson, J. P. (the late). (**Council**, 1896–1903)
Bidder, G. P., Sc.D., *Cavendish Corner, Hills Road, Cambridge.* (**Council**, 1899→; **President**, 1939–45; **Vice-President**, 1948→)
The Lord Moyne, P.C., D.S.O. (the late). (**Vice-President**, 1929; 1939–45; **President**, 1930–39)
Allen, E. J., C.B.E., D.Sc., LL.D., F.R.S. (the late) (Honorary.) (**Council**, 1895–1942; **Secretary**, 1895–1936; **Hon. Governor**, 1937–42)

FOUNDERS

1884 The Corporation of the City of London, *The Guildhall, E.C.* 3
1884 The Worshipful Company of Mercers, *Mercers' Hall*, 4 *Ironmonger Lane, E.C.* 2
1884 The Worshipful Company of Goldsmiths, *Goldsmiths' Hall, Foster Lane, E.C.* 2
1884 The Royal Microscopical Society, *B.M.A. House, Tavistock Square, W.C.* 1
1884 Bulteel, Thos. (the late)
1884 Burdett-Coutts, W. L. A. Bartlett (the late)
1884 Crisp, Sir Frank, Bart. (the late). (**Council**, 1884–92; **Hon. Treasurer**, 1884–88)
1884 Daubeny, Captain Giles A. (the late)
1884 Eddy, J. Ray (the late)
1884 Gassiott, John P. (the late)
1884 Lankester, Sir E. Ray, K.C.B., F.R.S. (the late). (**Hon. Secretary**, 1884–90; **President**, 1891–1929)
1884 Lord Masham (the late)

1884 Moseley, Prof. H. N., F.R.S. (the late). (**Chairman of Council**, 1884–88)
1884 Lord Avebury, F.R.S. (the late). (**Vice-President**, 1884–1913)
1884 Poulton, Prof. Sir Edward B., F.R.S. (the late). (**Council**, 1888–94)
1884 Romanes, Prof. G. J., LL.D., F.R.S. (the late). (**Council**, 1884–91)
1884 Worthington, James (the late)
1885 The 15th Earl of Derby (the late)
1887 Weldon, Prof. W. F. R., F.R.S. (the late). (**Council**, 1890–1901; representing British Association, 1901–5)
1888 Bury, Henry, *The Gate House*, 17 *Alumdale Road, Bournemouth West*
1888 The Worshipful Company of Drapers, *Drapers' Hall, E.C.* 2
1889 The Worshipful Company of Grocers, *Grocers' Hall, Princes Street, E.C.* 2
1889 Thompson, Sir Henry, Bart. (the late). (**Vice-President**, 1890–1903)
1889 Lord Revelstoke (the late)
1890 Riches, T. H. (the late). (**Council**, 1920–25)
1892 Browne, Mrs E. T. (the late)
1898 Worth, R. H., M.Inst.C.E., 32 *Thornhill Road, Plymouth, Devon*
1899 The Earl of Iveagh, C.B., C.M.G., 11 *St James's Square, S.W.* 1. (**Vice-President**, 1929→)
1902 Gurney, Robert, D.Sc., *Bayworth Corner, Boars Hill, Oxford*. (**Council**, 1932–5)
1904 Shaw, Joseph, K.C. (the late)
1909 Harding, Colonel W. (the late)
1910 Murray, Sir John, K.C.B., F.R.S. (the late). (**Council**, 1896–99; **Vice-President**, 1900–13)
1912 Swithinbank, H. (the late)
1913 Shearer, Dr Cresswell, F.R.S. (the late)
1913 Heron-Allen, E., F.R.S. (the late)
1918 Evans, George (the late). (**Hon. Treasurer**, 1915–31; **Vice-President**, 1925–33)
1920 McClean, Capt. W. N., 39 *Phillimore Gardens, W.* 8
1920 Lord Buckland of Bwlch (the late),
1920 Llewellyn, Sir D. R. (the late),
1921 Harmer, F. W. (the late)
1924 The MacFisheries, Ltd., *Ocean House, Pudding Lane, E.C.* 3
1924 Lady Murray (the late)
1925 The Institution of Civil Engineers, *Great George Street, Westminster, S.W.* 1
1925 Discovery Committee, *Colonial Office, Downing Street, S.W.* 1
1927 Bidder, Miss Anna M., Ph.D., *Cavendish Corner, Hills Road, Cambridge*. (**Council**, 1948→)
1933 Peel, Col. Sir Edward T., K.B.E., D.S.O., M.C., *c/o Messrs Peel and Co., Ltd., P.O. Box* 331, *Alexandria, Egypt*. (**Vice-President**, 1936→)
1938 Buchanan, Dr Florence (the late)
1945 Brown, Arthur W. W., *Sharvells, Milford-on-Sea, Hants*

MEMBERS

* Life Members

1939 Abercrombie, M., *Department of Anatomy, University College, Gower Street, London, W.C.* 1
1945 Aberdeen University Library, *The University, Aberdeen*

1941 Aberystwyth (*see* Wales)
1947 Achimota College, *Department of Zoology, Achimota, Gold Coast Colony*
1934 Adam, Mrs K. M. G., 21 *Belgrave Crescent, Edinburgh* 4
1940 Adrian, Prof. E. D., O.M., M.D., D.Sc., LL.D., F.R.S., *St Chad's, Grange Road, Cambridge*
1947 Affleck, R. J., 847 *Brighton Road, Purley, Surrey*
*1927 Amirthalingam, C., Ph.D., *Director of Fisheries, Colombo, Ceylon*
1932 Aquario Vasco da Gama, *Estação de Biologia Maritima, Cais do Sodré, Lisbon, Portugal*
1944 Ashby, D. G., *P.O. Avondale, Salisbury, S. Rhodesia*
1947 Astill, D. R. D., *Newball and Mason, Ltd., Beech Avenue, Nottingham*
*1911 Viscount Astor, 3 *Elliot Terrace, Plymouth, Devon* (**Vice-President**, 1911→)
1929 Atkins, Miss D., D.Sc., *Oak Cottage, Chichele Road, Oxted, Surrey*
*1939 Atkins, W. R. G., O.B.E., Sc.D., F.R.I.C., F.Inst.P., F.R.S., *The Old Vicarage, Antony, Torpoint, Cornwall*
*1910 Atkinson, G. T., *Apsley House, Esplanade, Lowestoft, Suffolk*

1948 Baal, H. J., 3 *Bel Royal Villas, Jersey, C.I.*
1939 Bahl, Prof. K. N., D.Sc., *Department of Zoology, The University, Lucknow, India*
*1920 Baker, J. R., D.Sc., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1936 Baldwin, E., Ph.D., *School of Biochemistry, Sir William Dunn Institute, Tennis Court Road, Cambridge.* (**Council**, 1946–48)
1939 Barnes, H., Ph.D., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1930 Barrett, W. H., *Roxeth Farm, Bessborough Road, Harrow, Middlesex*
1939 Barrington, E. J. W., *Department of Zoology, The University, Nottingham*
1946 Barter, W. Y., 29 *Sea View Avenue, Plymouth, Devon*
1939 Bassindale, R., *Department of Zoology, The University, Bristol*
1932 Bateman, J. B., Ph.D., *Physical and Chemical Division, Camp Detrick, Frederick, Ind., U.S.A.*
1946 Batham, Miss E. J., *c/o Department of Zoology, Downing Street, Cambridge*
1939 Baxter, E. W., *Biology Department, Medical School, Guy's Hospital, London, S.E.* 1
*1929 Bayliss, L. E., Ph.D., *Department of Physiology, University College, Gower Street, London, W.C.* 1
1934 Beadle, L. C., *Department of Biology, College of Medicine, University of Durham, Newcastle-upon-Tyne* 1, *Northumberland*
1928 Beer, Prof. G. R. de, D.Sc., F.R.S., *University College, Gower Street, London, W.C.* 1
1947 Berrill, Prof. N. J., *Department of Zoology, McGill University, Montreal, Canada*
1947 Best, A. C. G., 6 *Station Road, Loudwater, High Wycombe, Bucks*
1948 Betts, Slade, 100 *Avondale Road, Bromley, Kent*
1903 Bidder, Col. H. F., *The Malting House, Nettlebed, near Henley-on-Thames, Oxon*
1947 Bilton, Leslie, *c/o* 158 *Howard Road, Clarendon Park, Leicester*
*1945 Bingley, F. J., *Broomhill, Herringswell, near Bury St Edmunds, Suffolk*
1925 Birkbeck College, *Fetter Lane, London, E.C.* 4
1931 Birtwistle, W., 73 *North Street, Skibbereen, Co. Cork, Eire*
1947 Bishop, M. W. H., *Meadow Farm, Waterbeach, Cambs.*

1945 Black, J. A., *Ash House, Caton, near Lancaster, Lancashire*
1947 Black, Miss M. K., *c/o F. Band, High Street, Benwick, March, Cambs.*
1930 Blaschko, Dr H., *Department of Pharmacology, South Parks Road, Oxford*
1910 Bloomer, H. H., *Longdown, Sunnydale Road, Swanage, Dorset*
1936 Boguc, Prof. J. Yule, D.Sc., *Heyscroft, Hartley Road, Altrincham, Cheshire*
1932 Bolitho, Capt. R. J. B., *Gorey, Jersey, C.I.*
1945 Boney, A. D., *Ivydene, Grosvenor Road, Crownhill, Plymouth, Devon*
*1933 Boschma, Prof. Dr H., *Rijksmuseum van Natuurlijke Historie, Leiden, Holland*
1947 Bossanyi, J., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1944 Boyd, Lt. David, R.N.V.R., 261 *Woodstock Road, Oxford*
1940 Brambell, Prof. F. W. Rogers, D.Sc., *Department of Zoology, University College of North Wales, Bangor, Caernarvonshire.* (**Council**, 1944–47, 1948→)
1924 Brightwell, L. R., *White Cottage, Chalk Lane, East Horsley, Surrey*
1933 Bristol University, *Department of Zoology, Bristol*
1948 British Cod Liver Oils (Hull and Grimsby) Ltd., *P.O. Box No.* 18, *Hull*
1941 British Celanese Ltd., *Celanese House, Hanover Square, London, W.* 1
1939 British Ropes Ltd., *Western Avenue, Cardiff*
1946 Brough, Prof. James, D.Sc., *Department of Zoology and Comparative Anatomy, University College, Newport Road, Cardiff*
*1946 Brown, Miss C. H., *Girton College, Cambridge*
1928 Brown, Miss E. M., 6 *Effingham Lodge, Surbiton Crescent, Kingston-on-Thames, Surrey*
1936 Brown, Herbert H., O.B.E., Ph.D., *Manager, Fisheries Division, Colonial Development Corporation,* 33 *Dover Street, London, W.* 1
*1925 Bull, Herbert O., D.Sc., *Dove Marine Laboratory, Cullercoats, Northumberland*
1920 Burne, R. H., F.R.S., *Monkschester, Blue House Lane, Limpsfield, Surrey*
1948 Burrows, Mrs E. M., *Hartley Botanical Laboratories, The University, Liverpool* 3
1947 Burton, Miss J. M., 55 *Popes Grove, Twickenham, Middlesex*
1930 Burton, M., D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7. (**Council**, 1936–39)
1947 Burton, R. F., 55 *Popes Grove, Twickenham, Middlesex*

1920 Cannon, Prof. H. Graham, Sc.D., F.R.S., *Department of Zoology, Victoria University, Manchester.* (**Council**, 1927–30, 1932–34, 1937–41, 1942–45)
1927 Carruthers, J. N., D.Sc., *Hydrographic Department, Admiralty, Cricklewood, London, N.W.* 2. (**Council**, 1948→)
1923 Carter, G. S., Ph.D., *Department of Zoology, Downing Street, Cambridge*
1945 Carter, P., *Littlewood, Beadon Road, Salcombe, Devon*
1948 Carthy, J. D., 161B *Hills Road, Cambridge*
*1931 Cattell, Dr McKeen, *Cornell University Medical College,* 477 *First Avenue, New York City, U.S.A.*
*1948 Cattley, J. G., *Fisheries Laboratory, Lowestoft, Suffolk*
1936 Charterhouse School, *Biological Department, Godalming, Surrey*
1947 Cheng, Prof. Chung, Ph.D., *Department of Oceanography, National Amoy University, Amoy, China*
*1947 Chidambaram, K., *c/o Mr R. Vaidyalingom Pillai, Retd. Dewan Peishkar, Jagathy, Trivandrum, S. India*

1946 Chipperfield, Philip N. J., *Hillside, Manor Road, Brixham, Devon*
1942 Christie-Miller, Major E. G., 38 *Hyde Park Street, London, W.* 2. (**Hon. Treasurer**, 1941→)
1924 Clark, R. S., D.Sc., *The Cottage, Bieldside, Aberdeenshire.* (**Council**, 1938–41)
1947 Clarke, Miss D. H., *Hoe Garden House, Hoegate Street, Plymouth, Devon*
1944 Clarke, Robert H., *'Discovery' Investigations, Queen Anne's Chambers,* 41 *Tothill Street, London, S.W.* 1
1936 Clothier, Peter, *Hill Close, Street, Somerset*
1939 Clowes, A. J., *Division of Fisheries, Beach Road, Sea Point, Cape Town, S. Africa*
*1886 Coates and Co. (Plymouth), Ltd., *Black Friars Distillery, Southside Street, Plymouth, Devon*
*1945 Cobham, Lt.-Cdr. A. J., R.N., 44 *Strand-on-the-Green, London, W.* 4
*1925 Cockshott, Lt.-Col. A. M., R.A.S.C., *The Royal South Hants and Southampton Hospital, Centenary Appeal Office,* 105 *Graham Road, Southampton*
1933 Cole, H. A., *Fisheries Experimental Station, Castle Bank, Conway, Caernarvonshire*
1948 Collier, Albert, 826 *Maison Blanche Building, New Orleans, La., U.S.A.*
*1885 Collier and Co., 53 *Southside Street, Plymouth, Devon*
1947 Collis, Miss M. M., 27 *Mowbray Road, Cambridge*
1930 Colman, J. S., *Department of Zoology, The University, Sheffield* 10
1947 Cook, Miss P. M., 51 *Runnymede Crescent, Streatham, London, S.W.* 16
1940 Cook, R. H., 24 *Luard Road, Cambridge*
1939 Cooper, Major Brian, *Countess Weir House, Countess Weir, Exeter, Devon*
*1933 Cooper, L. H. N., D.Sc., F.R.I.C., *The Laboratory, Citadel Hill, Plymouth, Devon*
1937 Corbin, P. G., *The Laboratory, Citadel Hill, Plymouth, Devon*
1937 Corbin, Mrs P. G., *Dostabrook, Horrabridge, S. Devon*
1946 Corlett, John, M.Sc., *Fisheries Laboratory, Lowestoft, Suffolk*
1937 Cosway, C. A., 20 *Maurice Road, King's Heath, Birmingham* 14
1941 Cott, H. B., D.Sc., *University Museum of Zoology, Cambridge*
1948 Council for Promotion of Field Studies, *Dale Fort Field Centre, Haverfordwest, Pembs*
1936 Crawford, G. I., 18 *East Drive, Carshalton Beeches, Surrey*
*1928 Crew, Prof. F. A. E., M.D., D.Sc., F.R.S., *Usher Institute, Warrenden Park Road, Edinburgh* 9
1929 Crofts, Miss D. R., D.Sc., *Deerbank, Noisey Wood, Billericay, Essex*
*1930 Cuthbertson, Norman, *King's College School, Windsor, Nova Scotia, Canada*

1922 Dale, Sir Henry H., O.M., G.B.E., M.D., LL.D., F.R.S., *The Royal Institution,* 21 *Albemarle Street, London, W.* 1. (**Council**, 1922–28)
1948 Dales, R. Phillips, 67 *Westmoreland Avenue, Squirrels Heath, Essex*
1947 Dall, William, *Grace Street, Corinda, S.W.* 4, *Brisbane, Queensland, Australia*
*1919 Damant, Capt. G. C. C., C.B.E., R.N., *Thursford, Cambridge Road, East Cowes, I. of W.* (**Council**, 1928–31, 1937–40)
1939 Danielli, J. F., D.Sc., *Chester Beatty Research Institute, Royal Cancer Hospital, London, S.W.* 3. (**Council**, 1944–45)
1947 Danmarks Akvarium, *Charlottenlund, Denmark*
1929 Darby, Dr H. H., *Carnegie Institution of Washington,* 5241 *Broad Branch Road, N.W., Washington* 15, *D.C., U.S.A.*
1948 Dartmouth, The Royal Naval College

1946 Das, S. M., D.Sc., *Department of Zoology, The University, Lucknow, India*
1920 Davidson, Dr W. Cameron, *Avonleigh, Acadia Road, Torquay*
1943 Davies, D. J., 1 *Mayfield Terrace, Cwmburla, Swansea*
1931 Dawes, B., D.Sc., *Department of Zoology, University of London, King's College, Strand, London, W.C.* 2
1944 Day, Prof. J. H., D.F.C., *Department of Zoology, University, Rondebosch, Cape Town, S. Africa*
1948 Day, Lionel E., 24 *Inverness Avenue, Westcliffe-on-Sea, Essex*
1948 Day, Peter R., 36 *Templeton Avenue, Chingford, London, E.* 4
1938 Deacon, G. E. R., D.Sc., F.R.S., 55 *Broadhurst, Ashtead, Surrey*. (**Council**, 1946→)
1939 Dennell, Ralph, *Department of Zoology, The University, Manchester* 13
*1915 Dick, G. W., J.P., 500 *Manning Road, Durban, Natal, S. Africa*
1944 Digby, P. S. B., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1910 Dobell, C. C., D.Sc., F.R.S., *National Institute for Medical Research, Hampstead, London, N.W.* 3
1939 Dobson, A. T. A., C.B., C.V.O., C.B.E., *The Elms, Walsham-le-Willows, Bury St Edmunds, Suffolk*. (**Council**, representing Ministry of Agriculture and Fisheries, 1938–46)
1948 Dodd, J. M., *Gatty Marine Laboratory, The University, St Andrews, Fife*
1942 Dollner, H., 3516 *Northcliffe, Montreal, N.D.G., Canada*
1946 Douglas, Leslie, 11 *Harbour View, Seahouses, Northumberland*
1940 Dowson, Capt. W. B., *Agricultural Service, Nigeria, c/o Crown Agents for the Colonies,* 4 *Millbank, London, S.W.* 1
1946 Duly, S. J., 68 *Richmond Hill Court, Richmond, Surrey*
1939 Dundee University College Library, *Dundee, Forfar*
1947 Dunne, B., 53 *Headland Park, Plymouth, Devon*
1937 Dyke, Frederick Montague, *Branksome, Boreham Wood, Elstree, Herts*

1934 Eales, Miss N. B., D.Sc., *Zoology Department, The University, Reading*
1933 Eastham, Prof. L. E. S., *Department of Zoology, The University, Sheffield* 10
1945 Edgell, Vice-Admiral Sir John A., K.B.E., C.B., F.R.S., 1 *Glenalmond House, Manor Fields, Putney, London, S.W.* 15. (**Council**, 1945–48, **Vice-President**, 1948→)
1927 Eggleton, P., D.Sc., *Department of Physiology, The University, Edinburgh*
1928 Egypt: Coastguard and Fisheries Service, *Alexandria, Egypt*
1948 Elgood, J. H., 159 *Purley Oaks Road, Sanderstead, Surrey*
*1929 Elmhirst, L. K., *Dartington Hall, Dartington, near Totnes, Devon*
*1944 Elmhirst, Richard, *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1931 Enoch, C. E. D., *Rayman Lodge, Sherborne Road, Parktown, Johannesburg, S. Africa*
*1947 Evans, Miss G. C., *Gerrans, Portscatho, near Truro, Cornwall*
*1923 Evans, W. Edgar, 38 *Morningside Park, Edinburgh*
1942 Ewer, D. W., *Department of Zoology, Natal University College, P.O. Box* 375, *Pietermaritzburg, Natal, S. Africa*

1929 Faouzi, Dr Hussein, *Faculty of Science (Department of Zoology), Farouk I University, Moharram Bey, Alexandria, Egypt*
1922 Farran, G. P., *Knocklyon, Templeogue, County Dublin, Eire*. (**Council**, 1922–26)
1948 Faulkner, I. J., Ph.D., *I.C.I. Billingham Division, Billingham, F. Durham*

1933 Fellowes, Miss Rosalind, 23 *The Cloisters, Windsor Castle, Berks*
1940 Foote, Miss V. V. J., *Achimota College, Achimota, Gold Coast Colony*
1928 Ford, E., *The Laboratory, Citadel Hill, Plymouth, Devon*
1935 Ford, E. B., F.R.S., D.Sc., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1939 Forrest, J. E., *Department of Zoology, Queen Mary College, Mile End Road, London, E.* 1
1939 Fowell, R. R., *Municipal Technical College, Mount Pleasant, Swansea, Glam*
1912 Fox, Prof. H. M., F.R.S., *Bedford College for Women, Sussex Lodge, Regent's Park, London, N.W.* 1. (**Council**, 1928–30, 1931–34, 1944–47)
1942 Foxon, G. E. H., *Department of Biology, Guy's Hospital Medical School, London Bridge, London, S.E.* 1
1924 Fraser, Miss E. A., D.Sc., *Department of Zoology, University College, Gower Street, London, W.C.* 1
1935 Fraser, F. C., D.Sc., *British Museum* (*Natural History*), *Cromwell Road, London, S.W.* 7
*1935 Fraser, James H., *Marine Laboratory, Wood Street, Torry, Aberdeen*
*1939 Fretter, Miss Vera, Ph.D., *Department of Zoology, Birkbeck College, Fetter Lane, London, E.C.* 4
*1930 Fritsch, Prof. F. E., D.Sc., F.R.S., *Department of Botany, Queen Mary College, Mile End Road, London, E.* 1. (**Council**, 1931–34, 1937–40, 1943–46)
1948 Furness, W. J., *Inglewood, Abbey Park Road, Grimsby, Lincs.*

1941 Gardiner, Mrs A. C., *c/o Mrs Walter Gardiner*, 4 *Grange Road, Cambridge*
*1907 Garstang, Prof. W., D.Sc., *Five Elms, Apsley Road, Oxford.* (**Council**, 1907–10, 1923–28; **Vice-President**, 1940→)
*1928 Gates, Prof. R. R., D.Sc., LL.D., F.R.S., *Biological Laboratories, Harvard University, Cambridge* 38, *Mass., U.S.A.*
1948 Gatty Marine Laboratory, (The Principal), *The University, St Andrews, Fife*
1947 Gay, Miss M. V., *Lowerfield, Lapford, Devon*
1932 Ghardaqa Marine Laboratory of the Egyptian University, *Ghardaqa, Red Sea District, Egypt*
1947 Gibson, R. O., 3 *Gascoyne Place, Plymouth, Devon*
1935 Gilson, H. Cary, *Freshwater Biological Association, Wray Castle, Ambleside, Westmorland.* (**Council**, 1940–43, 1947→)
1945 Glasgow University, Zoology Department, *Glasgow, W.* 2
1946 Glover, R. S., *Department of Oceanography, University College, Hull*
1945 Goodland, W. S. L., 20 *Trinity Terrace, Weymouth, Dorset*
1939 Goodrich, Dr Helen Pixell, 12 *Park Town, Oxford*
1939 Gordon, Miss Isabella, D.Sc., *British Museum* (*Natural History*), *Cromwell Road, London, S.W.* 7
1943 Gourock Ropework Co., Ltd., 92 *Bay Street, Port Glasgow, Renfrew*
1931 Graham, Prof. Alastair, D.Sc., *Department of Zoology, Birkbeck College, Fetter Lane, London, E.C.* 4
1931 Graham, Michael, O.B.E., *Fisheries Laboratory, Lowestoft, Suffolk.* (**Council**, 1931–32, 1933–36, 1943–46)
1930 Gray, Sir Archibald M. H., C.B.E., M.D., F.R.C.P., F.R.C.S., 39 *Devonshire Place, London, W.* 1
1912 Gray, Prof. J., C.B.E., M.C., Sc.D., LL.D., F.R.S., *Department of Zoology, Downing Street, Cambridge.* (**Council**, 1920–24; representing Cambridge University, 1928–45; **President**, 1945→)

1943 Great Grimsby Coal, Salt and Tanning Co., *Fish Dock Road, Grimsby, Lincs*
1948 Grigg, Miss Ursula M., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1946 Gross, Fabius, Ph.D., *Department of Zoology, West Mains Road, Edinburgh*
1948 Grove, A. V., 48 *Carlton Terrace, Swansea, Glam*
1947 Guiler, E. R., *Department of Zoology, University of Tasmania, Hobart, Tasmania*
1947 Gundry, Joseph, and Co., *Bridport, Dorset*

1946 Haifa: *Sea Fisheries Research Station, P.O. Box 50, Haifa, Palestine*
*1946 Hamond, Richard, *Morston, Holt, Norfolk*
1947 Harbott, A. J., *Wensleydale,* 7 *Manorcrofts Road, Egham, Surrey*
1923 Hardy, Prof. A. C., D.Sc., F.R.S., *Department of Zoology and Comparative Anatomy, University Museum, Oxford.* (**Council**, 1938–41, 1942–45; representing Oxford University, 1946→)
1929 Harington, Sir Charles R., Ph.D., F.R.S., *National Institute of Medical Research, Mount Vernon House, London, N.W.* 3
1946 Harling, Miss K. E., *The Arches, Looe, Cornwall*
*1885 Harmer, Sir Sidney F., K.B.E., Sc.D., F.R.S., 5 *Grange Road, Cambridge.* (**Council**, 1895–1912, 1918–23; representing Royal Society, 1925–44; **Vice-President**, 1934→)
1932 Harris, Prof. J. E., Ph.D., *Department of Zoology, The University, Bristol.* (**Council**, 1946→)
1946 Harris, T. R., 31 *All Saints Road, Wyke Regis, Weymouth, Dorset*
1939 Harrison, R. J., M.R.C.S., L.R.C.P., *Vinicombe, The Woodlands, Farnborough, Kent*
1947 Harrow Lower School Biology Department, *Lower School of John Lyon, Harrow, Middlesex*
1929 Hart, T. J., D.Sc., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1934 Hartley, P. H. T., *Edward Gray Institute of Field Ornithology,* 91 *Banbury Road, Oxford*
1924 Harvey, H. W., Sc.D., F.R.S., *The Laboratory, Citadel Hill, Plymouth, Devon*
1933 Harvey, L. A., *Department of Zoology, University College of the South West, Exeter, Devon.* (**Council**, 1940–43)
1939 Hayes, Dr F. R., *Dalhousie University, Halifax, N.S., Canada*
1939 Hayes, Mrs F. R., *Dalhousie University, Halifax, N.S., Canada*
1948 Hedley, Ronald H., *Armstrong House, Meadowfield, Durham*
1931 Henderson, G. T. D., D.S.C., Ph.D., *Oceanographic Laboratory,* 23 *Sandport Street, Leith, Edinburgh* 6
1939 Henry, Dr Herbert G. M., *Doune Cottage, Macduff, Banffshire*
1925 Hentschel, C. C., 7 *Dudley Court, Upper Berkeley Street, London, W.* 1
1939 Herklots, G. A. C., Ph.D., *Vanners, Chobham, Surrey*
1939 Hewer, H. R., Assistant Professor, *Department of Zoology, Imperial College of Science, London, S.W.* 7
1926 Hickling, C. F., Sc.D., *Colonial Office, Sanctuary Buildings, Great Smith Street, London, S.W.* 1. (**Council**, 1947→)
1926 Hill, Prof. A. V., C.H., O.B.E., Sc.D., F.R.S., 16 *Bishopswood Road, Highgate, London, N.* 6. (**Council**, 1925–29, 1930–33, 1934–37, 1938–41, 1942–43; representing Royal Society, 1944→; **Vice-President**, 1948→)
1939 Hill, M. D., *Uplands, near Ledbury, Herefordshire*
1947 Hill, M. N., 6 *St Eligius Street, Cambridge*

1919 Hillier, W. T., M.R.C.S., 73 *Francis Road, Edgbaston, Birmingham*
*1921 Hindle, E., Sc.D., F.R.S., *Zoological Society of London, Regent's Park, London, N.W.* 8. (**Council**, 1946→)
1937 Hinton, M. A. C., F.R.S., 23 *Polworth Road, Streatham, London, S.W.* 16
1926 Hobson, Prof. A. D., *King's College, Newcastle-upon-Tyne* 1, *Northumberland*
1948 Hockley, A. R., *University College, Southampton*
1939 Hodgkin, A. L., F.R.S., *Trinity College, Cambridge*
1945 Hodson, W., *Rhodena, Penare Avenue, Prestatyn, Flints*
1947 Hollowday, E. D., F.R.M.S., 45 *Manor Road, Aylesbury, Bucks*
1948 Holme, N. A., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1946 Holmes, E. J., *Education Offices, Cobourg Street, Plymouth, Devon*
1939 Holmes, W., D.Phil., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1948 Holsgrove, H. E., 67 *Bridwell Road, Weston Mill Estate, Devonport*
1933 Horne, F. R., *National Institute of Agricultural Botany, Huntingdon Road, Cambridge*
1948 Howe, Surg. Lt.-Cdr. (D) D. C., R.N., *H.M.S. "Victorious" c/o G.P.O., London*
1932 Howes, N. H., *Department of Zoology, University College, Gower Street, London, W.C.* 1
1948 Human, A. H., C.B.E., 32 *Victoria Street, London, S.W.* 1
1928 Hunt, O. D., *Corrofell, Newton Ferrers, S. Devon.* (**Council**, 1944–47, 1948→)
1947 Hunter, W. Russell, *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
*1947 Hurrell, H. G., J.P., *Moorgate, Wrangaton, S. Devon*
1939 Hurst, C. P., *Landulph Rectory, Saltash, Cornwall*
*1920 Hutton, J. Arthur, *Woodlands, Alderley Edge, Manchester*
1912 Huxley, Julian S., D.Sc., F.R.S., *UNESCO*, 19 *Avenue Kleber, Paris* 16, *France.* (**Council**, 1920–25)

1946 Iceland: *Atvinnudeild Háskólans (Fiskideild), Reykjavik*
1945 Imperial Chemical Industries Ltd, *Nobel House*, 2 *Buckingham Gate, London, S.W.* 1

1945 Jefferies, H. S., 6 *Forester Road, Bath*
1935 Jenkin, Miss P. M., *Department of Zoology, The University, Bristol*
*1921 Jenkin, Mrs W., *Westhide, Hereford*
1934 Jepps, Miss M. W., D.Sc., *Department of Zoology, The University, Glasgow*
1937 Jersey: Conservateur honoraire du Musée de la Société Jersiaise
*1924 Jesus College, *Oxford*
*1947 John, C. C., D.Sc., *The Aquarium, Trivandrum, S. India*
1934 John, D. Dilwyn, D.Sc., *National Museum of Wales, Cardiff*
*1947 Johnson, D. S., 10 *St John's Road, Cambridge*
1944 Johnson, Dr F. R., *Osu Fisheries Station, P.O. Box* 630, *Accra, Gold Coast Colony*
1948 Jones, C. Burdon, *Department of Zoology, University College of N. Wales, Bangor*
1948 Jones, J. D., *c/o The Secretariat, Mauritius (ref. P/*891), *Mauritius*
1946 Jones, L. W. G., 28 *Dale Gardens, Mutley, Plymouth, Devon*
1946 Jones, N. S., *Marine Biological Station, Port Erin, Isle of Man*
1936 Jones, Rodney R. M., *Tros-yr-Afon, Penmon, Anglesey*

1946 Jones, Prof. R. V., C.B., C.B.E., D.Phil., F.Inst.P., *Department of Natural Philosophy, Marischal College, Aberdeen*
1947 Jörgensen, C. Barker, *Slettevej* 8, *Copenhagen Söborg, Denmark*
1923 Judge, J. J., *Virginia House, Palace Street, Plymouth, Devon*

1948 Katterns, L. B., 115 *Feltham Hill Road, Ashford, Middlesex*
1945 Katz, Max, 1915E, *Spruce Street, Seattle* 22, *Washington, U.S.A.*
1940 Keilin, Prof. D., Sc.D., F.R.S., *Molteno Institute, Cambridge.* (**Council**, 1940–43)
1946 Kelley, Major D. F., *Gulmarg, Elmsleigh Park, Paignton, Devon*
1946 Kenya: The Game Warden, *Game Department, P.O. Box* 241, *Nairobi*
1928 King, Mrs A. Redman, *Weetwood Hall, Leeds, Yorks*
1947 Kingsbridge Modern Secondary School, *Kingsbridge, S. Devon*
1927 Kirtisinghe, P., *Department of Zoology, University of Ceylon, Colombo* 3, *Ceylon*
1930 Kitching, J. A., O.B.E., Ph.D., *Department of Zoology, The University, Bristol*
1939 Knight, Miss Margery, D.Sc., *University Hall for Women Students, Holly Road, Fairfield, Liverpool.* (**Council**, 1943–46)
1945 Knowles, F. G. W., D.Phil., *Marlborough College, Marlborough, Wilts*
1938 Kollmann, Prof. M., *Bibliothèque de la Faculté des Sciences*, 40 *Allées Léon Gambetta, Marseille, France*
1948 Kow, Tham Ah, *c/o Fisheries Department*, 4*th Floor, Fullerton Building, Singapore*

*1925 Lebour, Miss M. V., D.Sc., *Kean Hill, Cawsand, near Plymouth, Devon*
1947 Lechane, J. D. B., 14 *Wyndham Street East, Plymouth, Devon*
1935 Le Mare, D. W., *Fisheries Department, Federation of Malaya and Singapore, Penang, Malaya*
1948 Letts, J. K., 183 *Windmill Lane, Greenford, Middlesex*
1948 Lloyd, A. T., *Wynona, Beacon Park Road, Plymouth, Devon*
1948 Lovegrove, T., 2 *Athenaeum Place, The Hoe, Plymouth, Devon*
1926 Lowndes, A. G., Sc.D., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1931 Lucas, C. E., D.Sc., *Marine Laboratory, Wood Street, Torry, Aberdeen*
1930 Lumley, Adrian, *Sunnyside, Castle Gardens, Torquay, Devon*
1938 Lysaght, Miss A. M., Ph.D., 6 *Cumberland Gardens, London, W.C.* 1

1938 MacDonald, R., 112 *Antrim Road, Belfast, N. Ireland*
1935 Mackenzie, Col. W., O.B.E., *c/o Messrs Peel and Co. Ltd., P.O. Box* 331, *Alexandria, Egypt*
1929 Mackinnon, Prof. D. L., D.Sc., *Department of Zoology, King's College, Strand, London, W.C.* 2. (**Council**, 1938–42)
1937 Mackintosh, N. A., D.Sc., 7 *Hinde House, Hinde Street, London, W.* 1. (**Council**, 1946→)
1947 Macnae, William, *Department of Zoology, University of Capetown, Rondebosch, C.P., S. Africa*
*1925 Magdalen College, *Oxford*
1945 Maitland-Adams, C. W., *The Old Rectory, Hawkwell, Hockley, Essex*
*1902 Major, H. G. T., 24 *Beech House Road, Croydon, Surrey*
1948 Mansfield, A. W., Inst.-Lieut. R.N., *N.H.Q. Trincomalee, Ceylon*
*1928 Manton, S. M., Sc.D., F.R.S. (Mrs J. P. Harding), 18 *Ennerdale Road, Richmond, Surrey*

1948 Marcotte, Alexandre, D.Sc., *Faculté des Sciences, Boulevard de l'Entente, Quebec, Canada*
1948 Mardon, Jasper, *Selwyn College, Cambridge*
1939 Marr, J. W. S., 28 *Cromwell Court, Kingston Hill, Surrey*
*1947 Marshall, Miss S. M., D.Sc., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1939 Matthews, L. Harrison, Sc.D., *Department of Zoology, The University, Bristol.* (**Council**, 1944–47)
1912 Maurice, H. G., C.B., 6 *St Mark's Square, Regent's Park, London, N.W.* 1. (**Council**, 1913–38, 1939–42; representing Ministry of Agriculture and Fisheries, 1927–38; representing Zoological Society, 1942→; **Vice-President**, 1948→)
1937 Mayne, Dr Cyril F., O.B.E., F.R.C.S., *c/o Barclays Bank Ltd., Plymouth, Devon*
1910 McClean, Capt. W. N., 39 *Phillimore Gardens, London, W.* 8
*1929 McEwen, Mrs Lawrence, 15 *Blackett Place, Edinburgh*
1945 McGill University, *Department of Zoology, Montreal, Canada*
1948 McIntyre, A. D., 96E *King Street, Helensburg, Dumbartonshire*
*1948 Menon, M. Devidas, *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1939 Metropolitan Water Board, 177 *Rosebery Avenue, London, E.C.* 1
1947 Miami University Marine Laboratory, *Coral Gables, Florida, U.S.A.*
1923 Milford Haven Trawler Owners Association, Ltd., *Milford Haven, Pembs*
1946 Miller, Cyril J., 42 *Westbourne Road, Peverell, Plymouth, Devon*
1947 Mitchell, E. S., *Fourlanesend Boys' School, Maker, near Plymouth, Devon*
1947 Mitra, G. N., *Assistant Director of Fisheries, Cuttack (Orissa), India*
1940 Moore, Hilary, Ph.D., *Woods Hole Oceanographic Institution, Mass., U.S.A.*
1948 Morgan, C. W., 11 *Clevedon Park Avenue, Milehouse, Plymouth*
1931 Mount Desert Island Biological Laboratory, *Salisbury Cove, Maine, U.S.A.*
1938 Mowbray, Louis L., *Curator, Bermuda Government Aquarium, Flatts, Bermuda*
1942 Moynahan, Dr E. J., *Wayside, Jordans, near Beaconsfield, Bucks*

1933 Neale, Morley H., *Chaffcombe House, Chard, Somerset.* (**Council**, 1934–36, 1939–42, 1943–46, 1947→)
1934 Neale and West, *Trawler Owners, Wharf Street, Cardiff*
1939 Needham, Joseph, Sc.D., F.R.S., *Gonville and Caius College, Cambridge*
1947 Newell, G. E., Ph.D., 11 *Wave Crest, Whitstable, Kent*
1947 Newton, Prof. Lily, Ph.D., *Department of Botany, University College of Wales, Aberystwyth, Cardigan.* (**Council**, 1947→)
1930 Nicholls, A. G., Ph.D., *Marine Biological Laboratory, Cronulla, N.S.W., Australia*
1947 Nisbet, R. H., 24 *Sheldon Avenue, Highgate, London, N.* 6
1948 Nobbs, Miss G. E. D., 4 *Clifton Estate, Plympton, Devon*
1948 Nunn, S. M., *The Laboratory, Citadel Hill, Plymouth, Devon*
1938 Nutman, S. R., *c/o* 179 *Rustlings Road, Sheffield* 11

1934 Oakley, Dr C. L., 58 *Cumberland Road, Bromley, Kent*
1930 Olive, G. W., *Dauntsey's School, West Lavington, near Devizes, Wilts*

1938 Oliver, James H., Ph.D., 16 *Southwark Street, London, S.E.* 1
1937 Omer-Cooper, J., *Zoological Department, Rhodes University College, Grahamstown, S. Africa*
1939 Ommanney, F. D., Ph.D., *c/o Post Office, Victoria, Mahé, Seychelles*
1947 Orr, A. P., D.Sc., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1910 Orton, Prof. J. H., D.Sc., F.R.S., *Department of Zoology, The University, Liverpool.* (**Council**, 1945–48)
1945 Otago University Library, *Dunedin, N. I., New Zealand*
*1928 Otter, G. W., *Southwood, Broadstone, Dorset*

1944 Pair Fishing Co., Ltd., *The Docks, Milford Haven, Pembs*
*1939 Panikkar, N. K., D.Sc., *University Zoological Laboratory, Triplicane P.O., Madras, India*
*1923 Pantin, C. F. A., Sc.D., F.R.S., *Trinity College, Cambridge.* (**Council**, 1930–32, 1933–36, 1937–40, 1941–44, 1945, representing Cambridge University, 1946→)
1941 Parke, Miss M. W., Ph.D., *The Laboratory, Citadel Hill, Plymouth, Devon*
1927 Parker, The Hon. John H., *Pound House, Buckland Monachorum, South Devon*
1937 Parry, D. A., Ph.D., *Department of Zoology, Downing Street, Cambridge*
1928 Parsons, C. W., *Zoology Department, The University, Glasgow*
*1920 Pass, A. Douglas, *Wooton Fitzpaine, Charmouth, Dorset*
1925 Pawlyn Bros., *Mevagissey, Cornwall*
1925 Pawlyn, T. A., *Mevagissey, Cornwall*
1929 Peacock and Buchan, Ltd., *Paint Manufacturers, Southampton*
1933 Peel, Col. Sir Edward T., K.B.E., D.S.O., M.C., *c/o Messrs Peel and Co. Ltd., P.O. Box* 331, *Alexandria, Egypt.* (**Vice-President**, 1936→)
1948 Peiping, Institute of Zoology, National Academy of Peiping, 58 *Museum Road, Peiping* 7, *China*
1939 Pennell, V., 28 *Huntingdon Road, Cambridge*
1925 Pentelow, F. T. K., *Old Slade Lane, Iver, Bucks*
1948 Pepper, H. C., *Hastings Aquarium, George Street, Hastings, Sussex*
1929 Percival, Prof. E., *Canterbury College, Christchurch, New Zealand*
1947 Perkins, E. J., *Cross Keys, Post Office, near Hereford*
1936 Perkins, F., *Red Hand Compositions Co.*, 2 *The Firs, York Road, Ripon, Yorks.*
1934 Picken, L. E. R., Ph.D., *Trinity College, Cambridge*
1940 Pike, R. B., Ph.D., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1906 Plymouth Corporation (Museum Committee), *Tavistock Road, Plymouth, Devon*
1910 Plymouth Education Authority, *Cobourg Street, Plymouth, Devon*
1906 Plymouth, Port of, Incorporated Chamber of Commerce, *Plymouth, Devon*
1924 Plymouth Proprietory Library, 1 *Alton Terrace, North Hill, Plymouth, Devon*
1929 Plymouth Public Library, *Tavistock Road, Plymouth, Devon*
1948 Pollard, D. G., 4 *Ferry Road, Devonport, Plymouth, Devon*
1939 Poole, H. H., Sc.D., *Royal Dublin Society, Ballsbridge, Dublin, Eire*
1947 Portsmouth Grammar School, *Biology Department*
1929 Portsmouth Municipal College, *Portsmouth, Hants*
1939 Potter, Miss E. A., *Westonbirt School, Tetbury, Glos*
1939 Pringle, J. W. S., *Department of Zoology, Downing Street, Cambridge*
*1947 Pryor, Thomas, D.S.O., *Westbourne House, Saltash, Cornwall*
1939 Pumphrey, R. J., Ph.D., *Department of Zoology, Downing Street, Cambridge*
*1939 Purchon, R. D., *Department of Zoology and Comparative Anatomy, University College, Newport Road, Cardiff*

1947 Queckett Microscopical Club (E. P. Herlihy, Hon. Sec.), 76 *Brook Green, London, W. 6*
1936 Queen Mary College, *Department of Zoology, Mile End Road, London, E. 1*
1939 Queen's University, *Belfast, N. Ireland*
1932 Quick, Dr H. E., F.R.C.S., 130 *Eaton Crescent, Swansea, Glam.*
1947 Qureshi, Q. H., *Department of Zoology, Imperial College of Science and Technology, Prince Consort Road, South Kensington, London, S.W. 7*
1932 Ramalho, Dr A., *Estação de Biologia Maritima, Cais do Sodré, Lisbon, Portugal*
1939 Rawlinson, Miss Ruth, 23A *Holbrook Road, Stoneygate, Leicester*
1947 Raymont, Prof. J. E. G., *Department of Zoology, University College, Southampton*
*1933 Rayner, G. W., *c/o C.S.I.R. Fisheries Division,* 1 *Museum Street, Perth, W. Australia*
*1936 Rees, W. J., D.Sc., 12 *Clive Road, Strawberry Vale, Twickenham, Middlesex*
1928 Reid, D. M., *The Science Schools, Harrow-on-the-Hill, Middlesex*
1947 Rendle, H. S., 5 *Radford Park Road, Plymstock, near Plymouth, Devon*
1935 Renouf, Prof. L. P. W., *University College, Cork, Eire*
1940 Richards, P. B., *c/o Lloyds Bank Ltd., Truro, Cornwall*
1946 Rifaat, Ahmed, *c/o Marine Laboratory, Fort Kait Bey, Alexandria, Egypt*
*1919 Ritchie, Prof. A. D., *Old College, The University, Edinburgh.* (**Council**, 1929–32, 1934–37)
1944 Ritchie, Prof. James, C.B.E., D.Sc., *Department of Zoology, The University, Edinburgh.* (**Council**, 1944–47)
1926 Robins, E. A., *Fairway, Stanley Road, Waterford, Lymington, Hants*
1948 Robinson, G. A., *Selwyn College, Cambridge*
1940 Rogers, Dr T. Howard, *Felden Oak Cottage, Felden, Hemel Hempstead, Herts*
1939 Ross, D. M., Ph.D., *Department of Zoology, University College, Gower Street, London, W.C. 1*
1939 Ross, Miss Sybil S., 10 *Midmar Gardens, Edinburgh* 10
1931 Rothschild, Rt. Hon. Lord, G.C., Ph.D., *Merton Hall, Cambridge.* (**Council**, 1939–42)
*1932 Rothschild, The Hon. Miriam (The Hon. Mrs George Lane), *The Cottage, Ashton Wold, Peterborough, Northants.* (**Council**, 1942–45)
1945 Rowett, Miss H. G. Q., *Plymouth Technical College, Tavistock Road, Plymouth, Devon*
1924 Rudge, Chas. H., *Four Winds, Gurnick, Newlyn, Penzance, Cornwall*
1922 Russell, E. S., O.B.E., D.Sc., *Cloisters, Three Oaks, Hastings, Sussex.* (**Council**, 1927–30, 1932–35, 1936–39, 1940–43; **Vice-President**, 1948→)
1927 Russell, F. S., D.S.C., D.F.C., F.R.S., *The Laboratory, Citadel Hill, Plymouth, Devon.* (**Secretary**, 1945→)
1948 Rutter, G. R. P., *Bradewick, Thorpe-le-Soken, Essex*

1927 St Aubyn, Capt. The Hon. Lionel, M.V.O., *Saltram, Plympton, Devon*
1946 Sagay, A. A. E., *University College, Exeter, Devon*
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